DEVELOPMENT OF A PASTURE MODEL

FOR

GRAZING STUDIES

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CONTENTS

3.2 THE NUTRITIVE VALUE OF PASTURE TO THE RUMINANT ANIMAL

Chapter Four

EXPERIMENT 1

An investigation into the sward structure and digestibility changes within an S24 perennial ryegrass sward throughout the year under four levels of nitrogen fertilization.

Chapter Five

EXPERIMENT 2

An experiment to examine the effect of the removal of particular leaves from the tiller on senescence (estimated by digestibility changes), and on re-growth, using three growth room environments.

Chapter Six

FORMULATION OF A PASTURE MODEL FOR GRAZING STUDIES

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DECLARATION

I declare that I have composed this thesis myself. The work embodied in it is the result of my own investigations except where reference has been made to published literature, or to unpublished information whose source has been acknowledged.

ABSTRACT

The object of this thesis was to study those aspects, mainly of pasture origin, which affect the herbage intake of the grazing ruminant.

Literature was reviewed on the growth of grass, its nutritive value, the manner in which pasture is grazed, and its regrowth after defoliation. The nutritive value of grass was examined largely in terms of its digestibility.

Two experiments were carried out to obtain quantitative information on sward structure and the digestibility of the components. The first experiment used S24 perennial ryegrass growing in field conditions. The weights, heights, digestibilities and ages of parts of the tiller were monitored throughout the year and under different levels of nitrogen fertilizer. The organic matter digestibility of the two youngest leaves (89% 1st leaf, 86% 2nd blade) varied to only a small extent with season. Major changes in leaf digestibility (from about 82% to about 65 or 70%) were associated with a change in colour from green to brown. Nitrogen fertilizer had a small temporary effect in increasing leaf appearance rate, reducing leaf lifespan, and reducing leaf digestibility. It had a substantial effect on the vertical distribution of dry matter in the sward.

The second experiment examined leaf growth and digestibility following the removal of a particular leaf or leaves from tillers of S24 ryegrass. The investigation took place in controlled environment rooms under three temperature regimes ($6^{o}C/3^{o}C$; $10^{o}C/4^{o}C$; $19^{o}C/4^{o}C$) and low light intensities ($40 - 90\ W\ m^{-2}$). There was a reduction in the weight of new leaves only when defoliation was severe and included the removal of the two youngest leaves. Digestibility was unaffected.

The discussion develops a conceptual framework for a grazing model. Pasture is represented in terms of the spatial distribution, weight and digestibility of its component parts. Some of the quantitative relationships are provided by the information obtained from the two experiments reported. The model provides a possible means of testing alternative hypotheses as to how the ruminant selects its diet.

CHAPTER ONE

INTRODUCTION

An agricultural system is the planned production of food or fibre through the growth of living organisms.

The motives behind the pursuance of this broad objective tend to be different at the farmer, national and international level. The farmer in the Western world has, in general, financial profit as his motive. At the national level, the efficient production of food using the nation's particular resources is regarded as important. Policies have been outlined by successive governments, most recently in the White Paper 'Food from our own Resources' (1975). The import-saving or export-earning rôles of agricultural production are brought into consideration. At the international level, the nutritional requirements of a balanced diet and the limits to the quantity of food that can be produced are recognized; attention is directed towards the production and distribution of food on a world scale (within the context of a finite and uneven distribution of resources).

The objectives stated for each of these levels are not mutually exclusive. Indeed the means of satisfying successively broader objectives must take into account those lower down in the hierarchy if they are to succeed. One country cannot supply another with a commodity if there is no benefit to the farmer in producing it.

As world populations increase there will be increasing competition for food resources. It has, therefore, become a matter of great importance that systems of food production be analysed, understood, and synthesised. There must be a robust framework of knowledge available within which decisions can be made.

The study, construction and management of agricultural systems requires:

(a) knowledge of the biological mechanisms and processes by which matter is converted from one form in the system into another;

(b) a means of expressing the mechanisms in relation to one another and to the whole system. Not only do biological systems involve a large number of components, they also operate at different levels ranging from detailed biochemistry to animal behaviour.

(c) a means of evaluating a system, whether it be in biological, resource utilization or financial terms.

Mathematical modelling provides a means whereby some of these objectives may be fulfilled.

The modelling of an agricultural system serves three main purposes. Firstly, and basically, it requires that a systematic and explicit structuring of the available knowledge and understanding of the components, mechanisms and processes in the system be carried out.

Secondly, it enables us to make decisions as to how the system can be managed in order to satisfy the purpose for which the system is designed. Trial decisions can be simulated in the computer; selected ones can be validated in the field.

Thirdly, it exposes gaps in knowledge and indicates where further research is required before the model can be made sufficiently robust to meet all purposes.

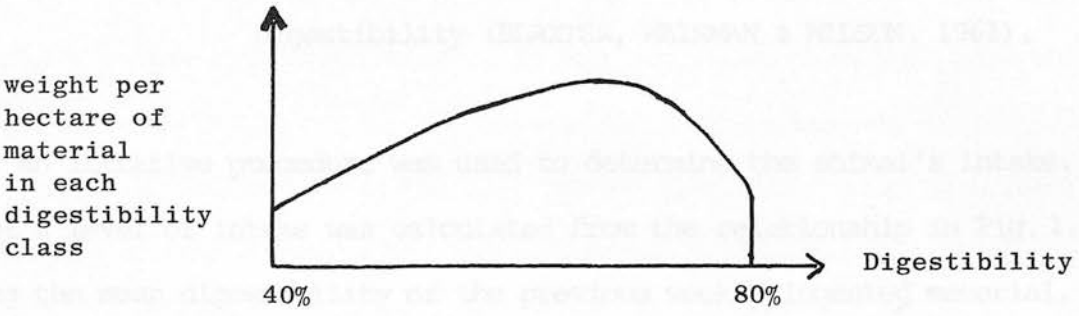
GRAZING SYSTEMS

Grazing systems are designed to harness the primary production of herbage to the secondary production of meat. Nutritional requirements of animals have to be met from seasonal changes in pasture growth.

The eventual transfer of radiant energy, carbon dioxide, water and minerals into animal products is dependent on the complex organisation of a large number of biological processes and environmental variables. A comprehensive, logical and explicit representation of a grazing system by a mathematical model can provide the basis from which to examine the effects of changes in the external variables.

Collaborative work was begun in 1973 at the Hill Farming Research Organisation, Edinburgh, to model sheep production from upland grazing systems. This thesis arose after preliminary work had highlighted major components upon which information was inadequate.

An initial model was built* using as its conceptual basis a pasture described in terms of digestibility units, e.g.



Growth of pasture was represented by adding new pasture into the top digestibility class. Ageing was simulated by moving a proportion of material from one digestibility class down into the next at a hypothetical rate. Material moving out of the lowest class was regarded as unavailable to the grazing animal.

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* T.J. Maxwell, A.R. Sibbald, J. Eadie, A. Vine.

Animals grazed this conceptual representation of the pasture according to certain hypotheses on diet selection. Their total intake per day was determined by the digestibility of ingested material according to the relationship:

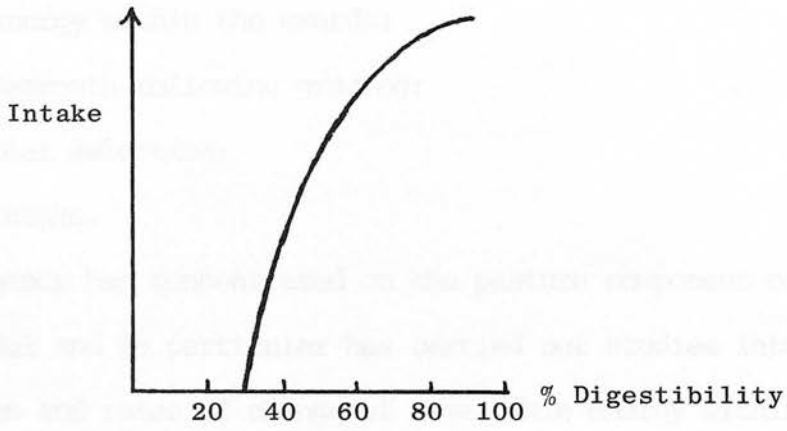


Fig. 1.1 : Relationship between voluntary intake and digestibility (BLAXTER, WAINMAN & WILSON, 1961).

An iterative procedure was used to determine the animal's intake. First a level of intake was calculated from the relationship in Fig. 1.1, using the mean digestibility of the previous week's ingested material. The animal was made to graze this quantity according to the selection rules. When complete, the actual digestibility of the animal's intake was calculated (D). If, according to Fig. 1.1, intake was greater than or less than it should have been at digestibility D, then the grazing process was repeated. The starting digestibility for predicting intake was altered to D as a closer approximation to the mean digestibility of ingested material. Iteration continued until estimates of intake and digestibility converged to within ±0.5% of the empirical relationship found by BLAXTER *et al*.

The digestible organic matter intake was converted into the growth and maintenance of wether sheep.

From a preliminary examination of the model, it became evident that too little was known about certain components which were crucial to the model's operation. These components were:

(i) Distribution and rates of change of digestible energy within the swards;

(ii) Regrowth following grazing;

(iii) Diet selection;

(iv) Intake.

The author has concentrated on the pasture component of the grazing model and in particular has carried out studies into the distribution and rates of change of digestible energy within the sward.

In the thesis, the units by which the pasture should be represented are considered first. It was concluded that the pasture should be modelled at the morphological level of leaves and tillers. The literature was reviewed for information that would help to build quantitative relationships for the conceptual model. It was found, however, that data on the structure of the sward and the digestibility of its component parts were completely inadequate. Experiments were designed and carried out to provide some of the information required. The results are discussed in relation to the literature and used to develop quantitative relationships for a modified version of the conceptual model.

CHAPTER TWO

CONCEPTUAL REPRESENTATION OF THE PASTURE COMPONENT IN GRAZING SYSTEMS

Units of Pasture Production

Pasture can be treated as a unit of production in itself: a surface area or leaf-mass that is photosynthesising, respiring and growing. Primary production is expressed as a function of parameters of the canopy - leaf area, leaf angle, photosynthetic response to light intensity, transmission of light through leaves (MONTEITH, 1965; DE WIT, 1965; ROBSON, 1973b).

The 'canopy' concept of pasture production can be refined by dividing the sward up into layers so that the decline in photosynthetic efficiency of leaves, as they age, can be taken into account (LEAFE, 1972). Net output from the pasture unit is expressed as total dry matter yield above ground level. This approach is applicable to conserved grassland and could also be used when considering the utilization of resources; for a grazed pasture situation it is only of interest as an indicator of potential seasonal or annual yield.

Alternatively, the pasture can be treated as a population of plants whose potential growth is limited by climate and by competition. Studies with spaced plants show the upper limits of production that can be achieved by an unrestricted individual plant in a given environment. Spaced plant trials of S24 perennial ryegrass have been carried out in the vicinity of Edinburgh by THOMSON & SEATON (1956); observations included growth habit, date of ear emergence, weight of dry matter at flowering, and leafiness of the regrowth.

When plants are grown together in a sward, the limiting factors to production become light interception, nutrient availability and water supply, as well as climatic factors. Investigations have been carried out into the effects of fertilizer levels and defoliation regimes on the growth and regrowth of pure and mixed stands of herbage species, e.g. McBRATNEY & LAIDLAW (1974).

This 'cultivation' approach differs from the 'canopy' approach in that it is more species specific and practically orientated, i.e. it is concerned with the limitations and responses of the particular genetic material that is avilable for cultivation. The object is to improve grassland management in terms of fertilizer usage, cutting and grazing regimes, and species used, bearing in mind their annual growth curves, competitive abilities and nutritional qualities. A certain amount of pasture modelling has been done at this level, for instance HEADY & DILLON (1961) present examples of models used in the economic and agronomic assessment of fertilizer response and use.

In contrast to the 'canopy' approach, however, the 'cultivation' approach is only descriptive. It cannot be directly incorporated into a general model of grassland growth in which the biological processes are simulated.

A further approach to the growth of pasture is as a population of tillers or leaves whose structure, development, physiology and organic matter production can be documented. A large amount of experimental work has been carried out seeking to understand the physiology and regulation of plant growth and senescence at the leaf or tiller level. Major references include MILTHORPE & IVINS (1966): 'The Growth of Cereals and Grasses', BUTLER & BAILEY (1973): 'The Chemistry and Biochemistry of Herbage, Vol. 2', and LEOPOLD & KRIEDEMANN (1975): 'Plant Growth and Development'.

Some modelling of pasture production has also been carried out at this level. For instance, YU, GINTZBURGER & GOUNOT (1975) incorporate a morphogenetic sub-model within their model of a vegetative population of cocksfoot. THORNLEY (1972) has built a model to describe the partitioning of photosynthate during vegetative plant growth.

Pasture production has, then, been analysed in a number of ways. The approaches differ in the objectives behind the studies and consequently in the unit(s) of production that they emphasise.

In portraying the pasture component of a grazing system, the following objectives must be met:

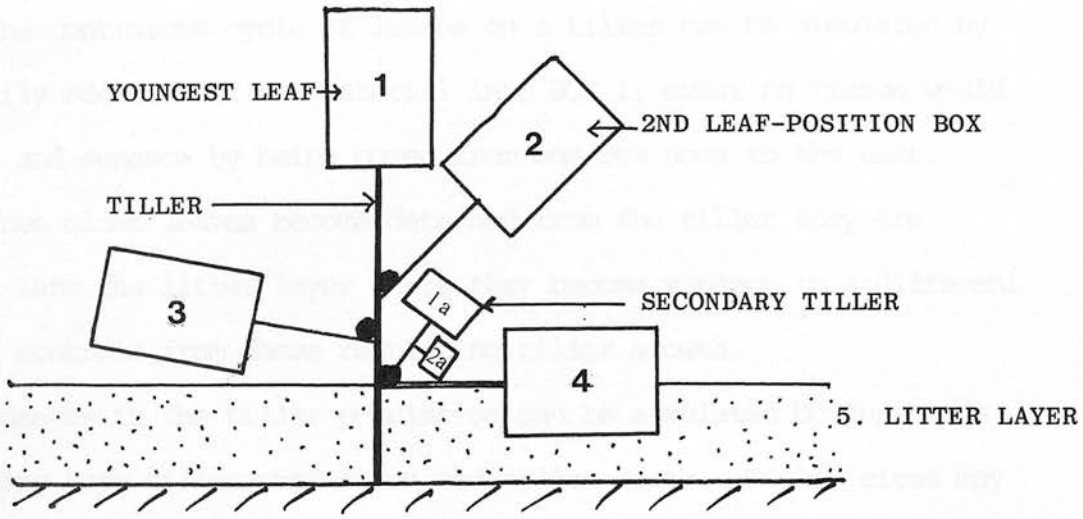
(i) herbage growth should be modelled in sufficient detail to allow the model to be operated under a wide range of conditions.

(ii) the pasture should be represented in a form to which the mechanics of grazing can be applied.

(iii) the responses of a pasture to being grazed should feed back into pasture growth and availability.

The unit of primary production used in the model must be one that is equally applicable to grazing. Since animals are reported as grazing certain plants or parts of plants more often than other plants or parts (ARNOLD, 1963; HODGSON, 1966), then the structure of the pasture must be represented at at least that level of morphological detail. If the type and quantity of tissue removed by grazing can be represented, then the dietary intake of the animal can be evaluated. The response of the plant to defoliation depends upon the type of tissue removed (e.g. young expanding leaf), as well as on the quantity. The description of the pasture in morphological units therefore enables more realistic simulation of the plant's response to being grazed.

To meet the objectives of a pasture model it was decided to examine the pasture as a population of tillers subtending leaves at different stages of growth, maturity and senescence. Initially leaves were classified into leaf-position boxes:



● = potential tillering sites, one of which has developed into a daughter tiller.

Each 'leaf-position box' may be examined and described in terms of:

weight

upper and lower height boundaries

digestibility

age.

Weight changes due to growth, translocation, respiration or movement of a leaf from one 'position' to the next (upon the appearance of a new leaf) could be described by the addition or subtraction of material to a leaf-position box.

The horizon in the sward occupied by a particular box is determined by factors which affect the lengths of the leaves in the box, and by the erectness of the leaves.

Digestibility may be investigated in relation to leaf position or leaf age.

The mean age of material in each box would be a function of leaf appearance rate.

The continuous cycle of leaves on a tiller can be simulated by the daily addition of new material into BOX 1; existing tissue would mature and senesce by being moved from one box down to the next.

When older leaves become detached from the tiller they are passed into the litter layer where they become subject to a different set of controls from those regulating tiller growth.

Changes in the tiller population can be simulated by functions governing both tiller production and tiller death. Tiller sites may be registered in association with each leaf-position box and allowed to develop into tillers only if certain nutritional, environmental and genetic conditions are satisfied.

Thus in this preliminary model the growth and senescence of pasture is partitioned into the morphological units found in the field. It provides a conceptual basis from which to develop a quantitative model that will meet the objectives set out on page 8.

CHAPTER THREE

LITERATURE REVIEW

INTRODUCTION

The requirements to be met by a model of the pasture component of grazing systems, as outlined in Chapters 1 and 2, set the context for the Literature Review. Literature was examined on the growth of grass, its nutritive value, the manner in which pasture is grazed, and re-growth of grass after defoliation. The review was carried out bearing in mind the purpose for which the knowledge and understanding received were ultimately to be used.

The numbering system used throughout the thesis for referring to leaves at different positions on the tiller is shown in Fig. 3.0:

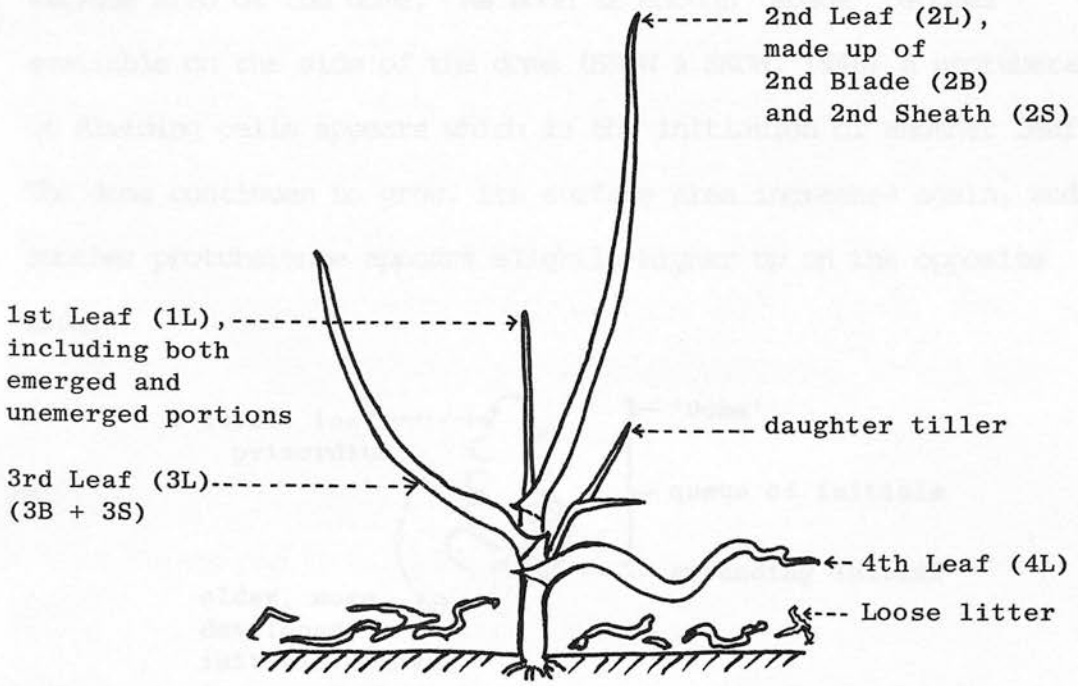


Fig. 3.0 : Symbols used in text for referring to different leaf positions.

In general, S24 perennial ryegrass is the variety used in the literature review to illustrate particular points.

3.1 THE GROWTH OF PASTURE

3.1.1 DEVELOPMENTAL ANATOMY OF A TILLER

Accounts of anatomical development in the Gramineae have been published by SHARMAN (1945) and ESAU (1965). SOPER & MITCHELL (1955-6) give a very useful account of the developmental anatomy of New Zealand perennial ryegrass with many drawings to illustrate the growth and tissue structure of leaves, roots and the vascular system.

Most of the initiation and development of shoot tissue in a vegetative grass tiller takes place in a very small region of the plant, within about 2 mm of ground level. This region, the apical meristem, is a dome of cells about 0.20 mm high x 0.13 mm wide that are continually dividing, tending to increase the free surface area of the dome. As soon as enough 'space' becomes available on the side of the dome (SNOW & SNOW, 1948) a protuberance of dividing cells appears which is the initiation of another leaf. The dome continues to grow, its surface area increases again, and another protuberance appears slightly higher up on the opposite side.

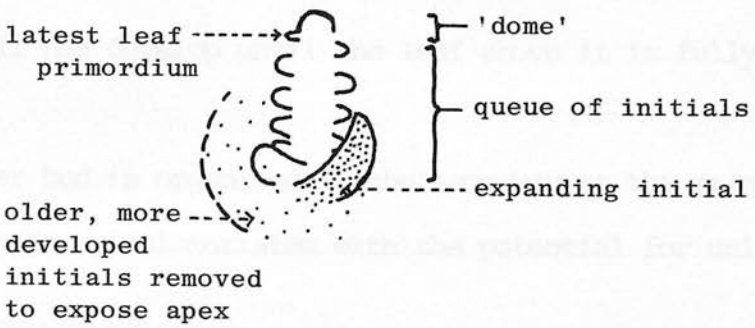


Fig. 3. 1 : The vegetative shoot apex of *Lolium perenne* (from COOPER, 1951).

Each new leaf primordium expands, encircles the apex, grows out into a cowl-like hood enclosing the apex and younger primordia, and elongates into a leaf.

By the time the leaf initial is about 1 cm long, cell division has become confined to a narrow band of tissue from which the ligule is just being formed, dividing the blade meristem from the sheath meristem. Some further growth by cell division takes place but most of the growth in length of the leaf is due to cell expansion. Cells start to expand as they move away from the meristem. As soon as they emerge from the surrounding sheaths into the daylight, they stop expanding (BEGG & WRIGHT, 1962). When the ligule appears, the leaf blade has reached its final length though not necessarily its final weight. The sheath continues growth for some time longer.

Associated with every leaf is a tiller bud which is formed on the opposite side of the stem soon after the leaf initial has appeared. Although the bud sits in the axil of the leaf below - as a result of internode elongation - it is more closely associated by ontogeny with the leaf above (ESAU, 1965). This may be relevant to MITCHELL's observation (MITCHELL, 1953a) that a tiller will not develop until the leaf above it is fully expanded.

A tiller bud is organised in the same way as the main stem apex; it is an apical meristem with the potential for unlimited growth.

The important features to note about leaf initiation and expansion are, firstly, that there is a continual succession of

leaf initials being produced and, secondly, that rates of initiation and elongation are largely determined by conditions in a very small part of the plant very close to ground level. These two features of leaf development in grasses have important physiological implications and may represent outstanding evolutionary adaptations of grasses to grazing.

The rate of production of tiller buds is also dependent upon conditions at the stem apex. Their subsequent development, however, is not a matter of course as it is with the leaves. Hormonal and nutritional factors can suppress their development.

3.1.2 THE GENETIC CONTROL OF LEAF AND TILLER GROWTH

Some mechanism exists which regulates the number of live leaves on a tiller to a very small number compared with the queue of initials waiting on the apex of the stem. In vegetative tillers of S24 ryegrass this number varies from 1.37 live leaves in winter to only 2.66 in spring (I. DAVIES, 1969) although at this time there is a considerable increase in light, temperature and nutrient availability. Under constant environmental conditions the number remains constant.

There is also some mechanism that tends to prevent the development of daughter tillers from the tiller buds, unless certain conditions prevail. In a review of possible control mechanisms leading to apical dominance over lateral buds, PHILLIPS (1975) concludes that the correlative signal is hormonal, not nutritional. Nutritional conditions do, however, have to be sufficient to allow the bud to develop once it is released from dominance. It seems that auxin, produced in the young leaves,

acts as the principal signal by maintaining a deficiency of cytokinin in the lateral buds, thus inhibiting their growth. Since cytokinins can be synthesised both in the roots (KENDE, 1965) and possibly in the lateral buds, the deficiency could be maintained in two ways: Auxin could influence the distribution of cytokinin from the roots to the shoot so that little of it goes to the tiller buds, particularly the younger ones; or auxin could act by inhibiting the use of cytokinin by the tissues of the tiller bud.

In either case it is important to note that hormones produced in one part of a plant can influence growth over some distance in another part of the plant. This being so, a change in the relative sizes of hormone-producing tissues might alter hormone ratios or concentrations in the tiller buds.

The complexity of the tillering response to environmental variables is partly due to their interactive effects on the nutritional state of the plant. However, the foregoing argument suggests that the complexity may also result from a change in the relative sizes of hormone-producing centres, altering the degree of apical dominance.

The continual correlated cycle of leaves on a tiller is a basic feature of grass growth and is too regular a phenomenon to be explicable solely in terms of competition for nutrients. I. DAVIES (1962) concludes from his experiments on the lifespan of individual leaves of S24 ryegrass, that there is some mechanism co-ordinating leaf lifespan and leaf appearance rate. Appearance of a new leaf and death of an older one were found to be closely associated in undisturbed swards growing in controlled environments (ROBSON, 1973a).

BEAN (1964) found that disturbance by defoliation affected the rate of leaf death (at least partly because there were fewer leaves remaining to senesce), but within seven weeks the rate of death once more equalled the rate of leaf appearance.

The apparent association between appearance rate, lifespan and death rate, which leads to a constant number of live leaves per tiller, suggests some common control of leaf growth rate and senescence rate at the genetic level.

Development in the leaf follows a pre-programmed sequence of events as the work of HEDLEY & STODDART (1972) demonstrates. They followed the patterns of protein synthesis in *Lolium temulentum* and observed peaks of activity: (a) during leaf expansion, corresponding to photosynthetic enzyme formation, (b) in the fully expanded leaf corresponding to the maximum attainment of chlorophyll content, and (c) at the onset of senescence corresponding to the elaboration or release of degradative enzymes. The 1st and 3rd peaks were sensitive to photoperiod, occurring faster in long days. The 2nd peak tended to occur at a fixed point after leaf emergence, approximately half-way through the total lifespan of the leaf.

Given a sequential production of enzymes, it may be that the rate of development of the leaf at one stage may affect the rate of events at a later stage in the sequence.

Structural changes accompany the sequence of development in a leaf and these are discussed later in relation to nutritive value.

Genetic control of development in the vegetative plant has been considered. A hormonal response to increasing daylength switches development in the apical meristem from vegetative to reproductive. The plants have to have reached a certain physiological stage of development before they respond to the photoperiod stimulus - in S24 ryegrass this stage is reached after the plants have been vernalized. A 9 to 11 hour photoperiod will then induce the processes leading to flowering (COOPER, 1951).

The change of a tiller to the reproductive condition has important bearings on pasture production. One is that the tiller will cease to produce any more leaf initials since the dome of the meristem differentiates into the terminal spikelet of the inflorescence. The tiller thus dies after seed-setting, or earlier if the apex is removed by grazing or cutting.

Another result of reproductive tiller development is a great increase in dry matter production. LEAFE, STILES & DICKINSON (1974) have analysed the causes leading to greater dry matter production from flowering swards compared with vegetative. Both the rate of assimilate production and the subsequent partition of it between shoot and root growth differed. It appears that the canopy in a flowering sward makes more efficient use of the incident light partly because successive individual leaves maintain a higher photosynthetic efficiency than they do in a vegetative sward. This is favoured by the comparative lack of shading that expanding leaves on a flowering tiller experience as they develop (WOLEDGE, 1973). The capacity for high rates of photosynthesis developed in unshaded leaves is utilized, as ONG & MARSHALL (1975) have demonstrated. They showed that photosynthetic rates of upper leaves on

reproductive tillers increase as the demands of the growing seed create a large sink for photosynthates. In grass systems, however, the large quantity of assimilate being generated and utilized begins to contribute adversely to the nutritive value of the crop beyond a certain developmental stage (see sections 3.2.4.3 and 3.2.4.4).

The increased net photosynthesis of the flowering canopy relative to vegetative ones appears also to be related to the disposition of leaves within the canopy (LEAFE *et al.*, 1974).

However, although reproductive tillers lead to greater crop growth rates, they exert strong apical dominance during early growth (LANGER, 1974). Many of the vegetative tillers present, die, possibly as a result of competition; the number of tillers remaining per unit area following seed formation is therefore small, compared with a frequently cut sward (LANGER, RYLE & JEWISS, 1964).

Control over the sequence of development in leaves, and hormonal influences on tillering, probably operate at the genetic level as transcription from different genes is switched on and off (JACOB & MONOD, 1961; WOOLHOUSE, 1967; SUTCLIFFE, 1972).

Rates of development and the sizes of leaves and tillers will also be determined by the environment since this both influences hormone production (LEOPOLD & KRIEDEMANN, 1975, Chs. 15, 16, 17) and has a direct effect on the nutritional status of the plant.

3.1.3 THE ENVIRONMENTAL CONTROL OF PASTURE GROWTH

The parameters of grass growth most important with respect to gross dry matter production are:

(i) rate of leaf appearance

(ii) leaf weight

(iii) number of tillers.

Rate of senescence is related to leaf lifespan and is an important factor in the consideration of pasture utilization. It affects both the net production of dry matter that is available to the grazing animal, and the nutritive value of the pasture.

The responses of leaf appearance rate, leaf lifespan, leaf weight and tiller number to the environment are briefly outlined.

3.1.3.1 LEAF APPEARANCE RATE

Leaf appearance rate is the number of leaves appearing on a tiller per unit time. Rate of leaf appearance in the Gramineae has been well reviewed by ANSLOW (1966) and SILSBURY (1970).

Temperature has a large effect on leaf appearance rate as one would expect since a 10°C rise in temperature doubles the rate of enzyme reactions. In perennial ryegrass, temperature is only limiting when low. Leaf appearance rate increases slowly between 13°C and 24°C, after which it begins to decline:

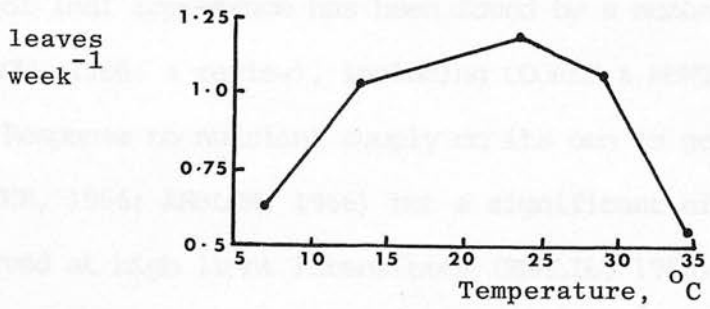


Fig. 3.2 : Number of leaves appearing per tiller per week (MITCHELL, 1956-7).

The effect of photoperiod is unclear. In general, experiments comparing constant photoperiods have found little effect of photoperiod on leaf appearance rate (COOPER & McWILLIAM, 1966; RYLE, 1966 ; ROBSON, 1967). However, outdoors under natural winter conditions ROBSON found that the slowest rate of leaf appearance in *Festuca arundinacea* occurred in mid-December. Thereafter it increased although temperature still remained low. PATEL & COOPER (1961) also suggest, from multiple regression analysis on seasonal changes in leaf appearance rate, that day-length is an important controlling factor.

Other environmental factors may limit leaf appearance only when they affect the availability of minerals or soluble carbohydrates to the terminal meristem. Since assimilates are transported preferentially to the stem apex and young expanding leaves (BEGG & WRIGHT, 1964; RYLE, 1970b), rate of leaf appearance is unlikely to be related to assimilate production except when this is very low. Thus MITCHELL & COLES (1954-5) obtained a 16% reduction in leaf appearance rate in plants shaded to 70% of daylight, and a 40% reduction if the plants were also defoliated so that an even smaller amount of light energy was intercepted. SILSBURY (1970) suggests that a marked response to light energy may only occur when intensities are low. However, an increased rate of leaf appearance has been found by a number of people (ANSLOW, 1966: a review), including COOPER & McWILLIAM (1966).

Response to nutrient supply on its own is generally small (LANGER, 1966; ANSLOW, 1966) but a significant effect has been observed at high light intensities (KHALIL, 1956). Unlike other people, I. DAVIES (1969) found the leaf appearance rate almost

doubled immediately after nitrogen fertilizer application in the field but the effect was only transient. It may have reflected a generally low nitrogen content in the soil but there is no evidence on this.

Leaf expansion is very sensitive to water stress (WESSELIUS & BROUWER, 1972), so it may be that leaf appearance from the enclosing sheaths is slowed down during periods of soil moisture stress.

3.1.3.2 LEAF WEIGHT AND LEAF SIZE

Little information has been published with respect to the effect of the environment on the maximum weight attained by a leaf (after growth in length has ceased but before any weight loss due to senescence has begun). SILSBURY (1970) found a fairly small increase in weight with increasing light intensity, and a substantial decrease in weight between the high temperatures of 20°C and 30°C.

However, leaf size - and in particular leaf length - is correlated with leaf weight (BAKER & JUNG, 1968) so it is possible to assess some of the effects of the environment on leaf weight by their effects on leaf size. SILSBURY (1970) concluded from his review of leaf growth that there were complex interactions operating between all the environmental and intrinsic factors affecting leaf size.

Leaf size is determined by cell number and cell size, both of which are largely controlled by conditions at the stem apex. MITCHELL & SOPER (1958), for instance, found that leaf width was mainly governed by the number of cell rows across the leaf, and this was

determined by the circumference of the sub-apical meristematic zone. At high temperatures plus low light intensities the sub-apical zone was narrow, perhaps due to a lack of available carbohydrate.

The length of both blade and sheath is related both to the rate of increase in cell length, relative to the duration of extension growth, and to cell number along the leaf (ROBSON, 1969). Both these factors are influenced by temperature. WILLIAMS & BIDDISCOMBE (1965) found great variation in the rate of extension growth, which was highly correlated with temperature but not light energy. Rate of increase in cell size is positively and highly correlated with temperature at the stem apex (PEACOCK, 1975b). Since large temperature gradients can exist within a few millimetres of ground level, the exact location of the stem apex is critical in the response of the plant to its environment (PEACOCK, 1975a).

In general, ROBSON (1969) concludes that long days tend to lead to longer and sometimes wider leaves, high light intensities to shorter but sometimes wider leaves, and high temperatures to longer but sometimes narrower leaves.

Not only does water stress result in a rapid decrease in the rate of leaf expansion, it also leads to a reduce rate of photo-synthesis which may eventually decline to zero. Respiration rate is unaffected at first but then it too declines (WESSELIUS & BROUWER, 1972). Prolonged periods of water stress might, therefore, be expected to result in shorter leaves with, possibly, a lower dry weight.

The mature weight of grass leaves is increased by nitrogen (RYLE, 1964; WILMAN, DROUSHIOTIS, MZAMANE & SHIM, 1977) and

other minerals (LANGER, 1966). However, the total increase in yield after nitrogen application ia mainly a result of increased tillering.

3.1.3.3 TILLER NUMBER

If every tiller site opposite every leaf developed into a tiller, then the rate of tiller production would be exponential and would be determined by the environmental factors governing the rate of leaf appearance. Each tiller bud would develop into a new tiller when the leaf above it had fully expanded (MITCHELL, 1953a; RYLE, 1964).

However, it has been shown that tiller buds are subject to apical dominance probably mediated by "Hormone-Directed Transport" (WENT, 1939; LANGER, 1974; PHILLIPS, 1975: see section 3.1.2) in which the materials necessary for growth are transported preferentially to the apical meristem and growing leaves. The effectiveness of apical dominance varies with the physiological and nutritional status of the plant, being more stringent during stem elongation (LANGER *et al*, 1964; LANGER, 1974) unless regularly supplied with nitrogen fertilizer (ASPINALL, 1961).

Within the framework of tiller-site production, and the limitations imposed by apical dominance, tillering is proportional to the amounts of energy substrate and mineral nutrients in the plant (MITCHELL, 1953b). Reviews of the environmental factors affecting tiller production in the Gramineae are given by MITCHELL (1953b) and LANGER (1963). The correlated interaction between environment, assimilate distribution and hormonal growth regulators on tiller bud growth is outlined by LANGER (1974).

Light has a major effect on tillering through its control over the photosynthetic production of soluble carbohydrates. Light and temperature interact, by their effects on the relative rates of photosynthesis and respiration, to determine the level of energy substrate in the plant. Since the rate of respiration increases faster than the rate of photosynthesis with increasing temperature, higher temperatures lead to lower levels of soluble carbohydrate. The temperature optimum for tillering varies with genotype (LANGER, 1963) and represents a balance between an increased formation of tillering sites and a reduced level of energy substrate. In young New Zealand perennial ryegrass plants the optimum was found to lie between 13^{o}C and 18^{o}C (MITCHELL, 1956-7). Light, on the other hand, continues to promote tillering as radiant energy increases (MITCHELL, 1953b).

Mineral nutrients also have a strong effect on tillering. Nitrogen is the most limiting but there is a marked response to phosphorus and potassium when the nitrogen level is adequate (LANGER, 1966). Nitrogen also interacts with light (LANGER, 1963, quoting RUSSELL, 1960) to promote tillering - partly as a result of the combined effect of nitrogen and light on rate of leaf appearance (KHALIL, 1956) and therefore number of tillering sites.

The observation by ASPINALL (1961), that a weekly supply of nitrogen prevented tillering from falling off at the reproductive stage, suggests that nitrogen supply may limit assimilate utilization by lateral buds at a given light intensity. Available nitrogen is generally only present in the soil for a short length of time and is soon taken up by plants or leached out of the soil. The burst of tillering following nitrogen fertilizer application

(I. DAVIES, 1969) shows how quickly the plant can respond to an increased supply of nitrogen.

Of all the parameters involved in determining dry matter production per unit area, tillering appears to be the one most sensitive to nitrogen supply (A. DAVIES, 1971a). In August 4 Kg N ha^{-1} day^{-1} was required for maximum dry matter production; above this level, although there was little increase in yield there was still a marked increase in tiller number. Below 4 Kg N ha^{-1}. day^{-1}, leaf number per tiller and leaf appearance rate were slightly reduced but the growth parameter particularly affected was again tiller number.

Plant growth in the sward

The effect of nitrogen supply on the growth of an individual tiller and on the production of new tillers, as outlined above, together with many other examples, emphasizes the statement by RYLE (1964) that "... external conditions may have played some part in shifting the balance of growth from tillering to leaf production and expansion. At all times there must be a partition of assimilates in the plant between the production of new shoots and the expansion of existing leaves and stems .... This partition is presumably controlled by growth substances in the plant, themselves influenced by environmental conditions and genetic factors."

The density of plants in the sward has a marked effect upon rates of leaf appearance and expansion (SILSBURY, 1970, quoting from the work by KLOOT, 1967, on ryegrass seedlings); on tillering (LANGER, 1963 - a review); and on the potential photosynthetic capacity of leaves (WOLEDGE, 1973). These effects may be understood

in terms of competition for, and partition of, the materials and energy for growth.

3.1.4 SEASONAL PRODUCTION OF GRASS

Every grass variety has a characteristic pattern of dry matter production which varies a little from year to year and under different management practices. The seasonal pattern of growth and dry matter production affects the suitability of the variety to a particular production system. The growth habit of the plant, its nutritional quality, and its response to severity and method of utilization, are all factors which need to be considered with regard to its use in animal production systems.

Annual 'growth curves' are standard items of investigation when testing grass varieties. Seasonal production tables and growth curves have been published by I.V. HUNT (1957), ANSLOW & GREEN (1967), and GREEN, CORRALL & TERRY (1971) for a large number of varieties including S24 perennial ryegrass.

The 'growth curve' gives the rate of net dry matter production by the crop at different times of the year. It is derived from measurements of the standing crop cut at a certain height above ground level at regular intervals of time. The yield at any one time is determined by the date of the previous cut, the rate of production of new material since then, the rate of weight change with senescence, and the rate of movement of dead material into the 'stubble' layer below cutting height. We have seen that pasture is a dynamic entity, a continual turnover of new leaves appearing and old ones dying, new tillers appearing and tillers dying. The rates of these changes were shown earlier to be governed by the environment

and by the physiological and nutritional state of the plant.

I. DAVIES (1969) has measured the rates of leaf appearance throughout the year in S24 under field conditions:

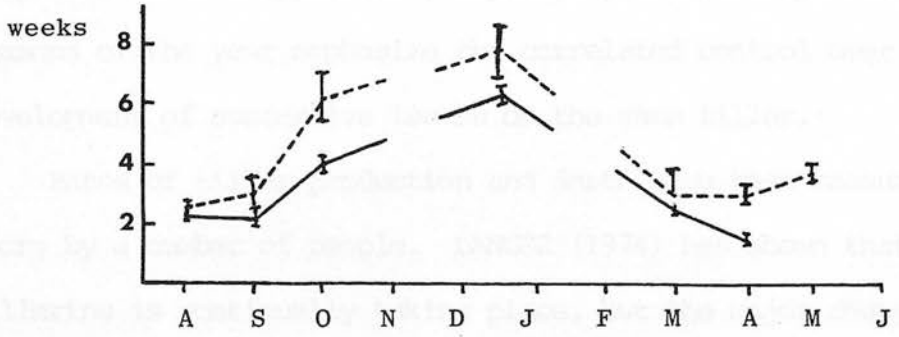


Fig. 3.3 : Leaf appearance interval of S24 ryegrass.

--- vegetative tillers

—— tillers which became reproductive in spring.

(I. DAVIES, 1969).

DAVIES followed the subsequent expansion and deaths of the same leaves:

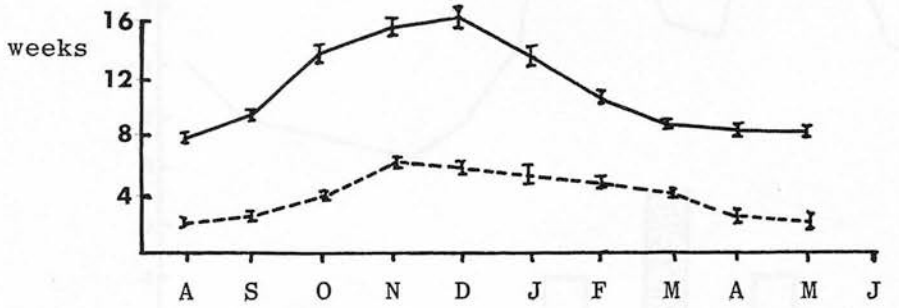


Fig. 3.4 : S24 ryegrass.

--- Time from first appearance of blade to full expansion.

—— Blade lifespan from first appearance to complete loss of green colouration.

(I. DAVIES, 1969).

Blade life-span follows the same pattern as leaf appearance. The time taken by the blade to reach full expansion also has a similar relationship, though less pronounced. The parallel responses of leaf appearance, expansion, and life-span to the seasons of the year emphasize the correlated control over the development of successive leaves on the same tiller.

Rates of tiller production and death have been measured outdoors by a number of people. LANGER (1974) has shown that tillering is continually taking place, but the major changes in the tiller population take place at certain times of the year (LANGER *et al*, 1964; GARWOOD, 1969).

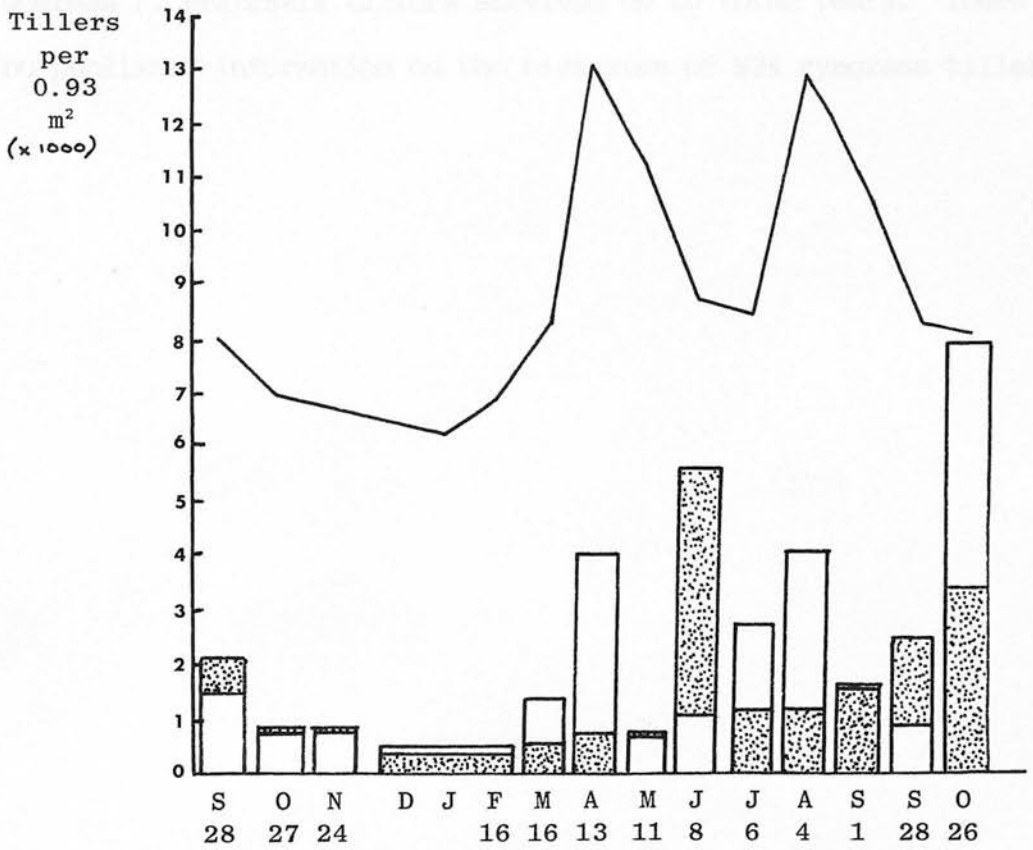


Fig. 3.5 : The changing tiller population of S24 ryegrass cut once every 4 weeks between April and October, (adapted from GARWOOD, 1969).

—— total number of tillers per 0.93 m^2 (x 1000)

no. of new tillers formed per month per 0.93 m^2 (x 1000)

no. of tillers dying per month per 0.93m^2 (x 1000)

The peaks in dry matter production do not correspond with those of vegetative tiller production, but they do correspond with the development of reproductive tillers in the sward.

The length of time that a tiller survives depends partly on the time at which it was formed, partly on whether and when it becomes reproductive, partly on competition and partly on such factors as disease (JEWISS, 1966). JEWISS followed the life histories of *Phleum pratense* and *Festuca pratensis* tillers in swards used for hay production, and in frequently cut swards. The life-span of a tiller varied with cutting regime, month of appearance and species. *P. pratense* tillers lived one year at most whereas *F. pratensis* tillers survived up to three years. There is no published information on the histories of S24 ryegrass tillers.

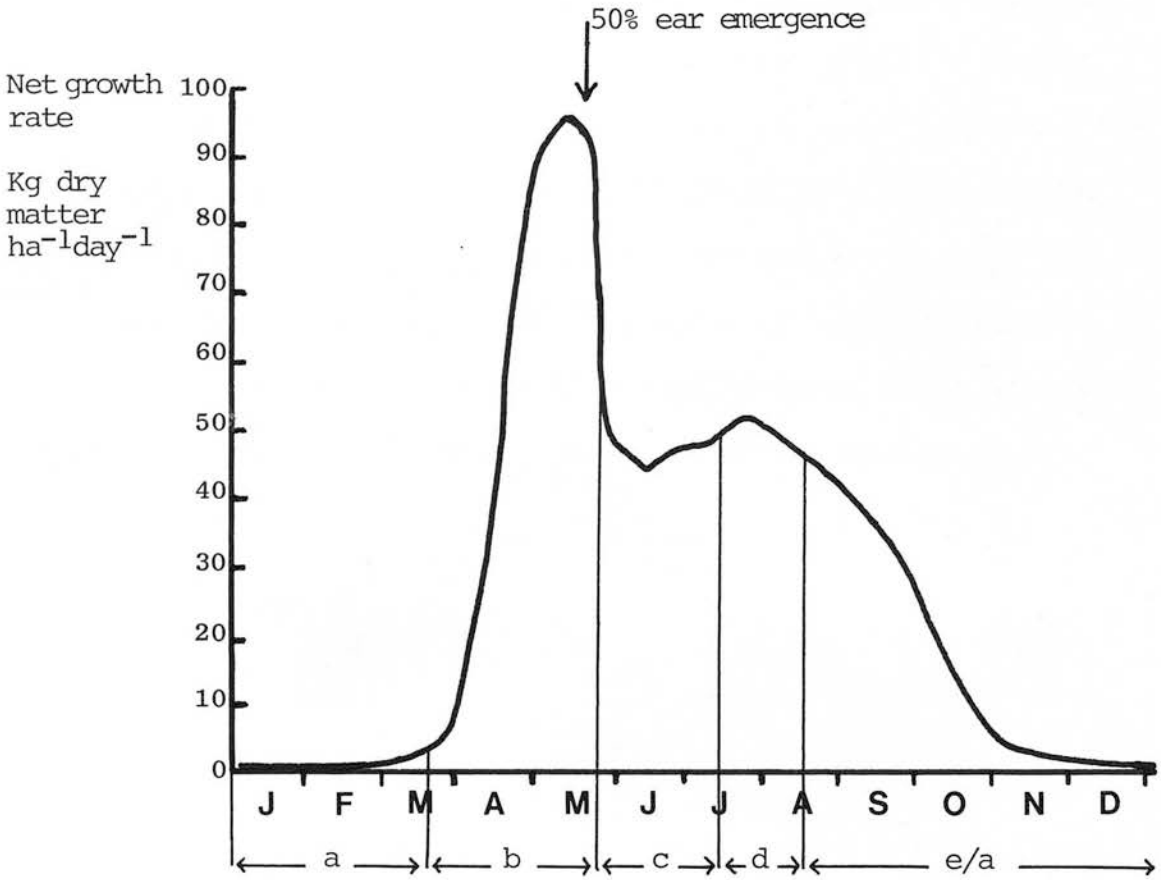


Fig. 3.6 : Rate of net production of S24 ryegrass, Hurley 1964. (ANSLOW & GREEN, 1967).

ANSLOW and GREEN (1967) have produced a growth curve for S24 perennial ryegrass whose shape can be analysed in five sections:

(Fig. 3.6)

a.	Slow leaf turnover.	
	Weight of new leaf = wt. of dying leaf (= 9 Kg ha^{-1} day^{-1} in New Zealand perennial ryegrass, HUNT, 1965).	no net production
	Little tiller turnover.	
b.	Soil nitrogen released above 5°C as nitrifying bacteria become active.	
	Ground level temperature rises above "minimum temperature for net growth", 5.5°C.	
	Faster rate of leaf appearance.	
	Leaves increase in size and weight. Wt. of new leaf > wt. of dying leaf (A. DAVIES, 1971b).	
	Few tiller deaths but quite a few new tillers produced.	
	Accelerating production as many tillers become reproductive (accelerates at 2.2 Kg ha^{-1} day^{-1} up to a net crop growth rate of 95 Kg ha^{-1} day^{-1} in early May, ANSLOW & GREEN, 1967)	50% ear emergence: 20 May (Hurley) 26 May (Edinburgh)
	After stem elongation, a large number of vegetative tillers die and new ones appear.	
c.	No reproductive tillers.	'Midsummer trough'
	Leaf appearance relatively unchanged.	
	Mean weight of a mature leaf no longer increasing much? (ALBERDA & SIBMA, 1968)	
	Decline in net rate of photosynthesis? (LEAFE, 1972)	
	Continuing high rates of tiller production and death.	
d.	Second phase of reproductive tiller growth, but constitutes a smaller % of the sward than in May.	second, much smaller, peak of production
e./a.	Slowing down of leaf appearance. Fewer leaves/tiller.	
	Small peak in tiller production at the end of October, but generally declining rates of tiller death and tiller production.	decline to no net production
	Availability of soil-nitrogen declining as soil temperatures fall below 5°C. Much shorter, duller days; cold temperatures, wind and frost.	

The growth pattern of a pasture has been related to the physiological stage, or growth form, of the plant, the environment, and the plant's nutritional status. Very broadly, the physiological stage is controlled by hormonal responses to the macro-environment, particularly to photoperiod; leaf appearance rate, leaf extension and leaf size are functions of the micro-environment at the stem apex; leaf size and tillering are proportional to the nutritional status of the plant.

3.2 THE NUTRITIVE VALUE OF PASTURE TO THE RUMINANT ANIMAL

3.2.1 INTRODUCTION

Systems of animal production in which ruminants obtain their main source of nutrients by grazing are an important feature of agricultural production in Britain and Ireland.

The amount of pasture ingested by an animal depends partly on characteristics of the sward (plant species, palatability, morphology, weight of standing crop) which are determined by grazing management and environment; partly on factors affecting the rate of passage of material out of the rumen (plant species and tissues ingested, rumen microbial activity); and partly on the species of animal grazing the pasture and its physiological status (e.g. lactating).

The actual nutrient intake depends in turn on both the amount of pasture ingested and on the efficiency with which the material is digested. Efficiency of digestion is related both to aspects of the animal's digestive process (e.g. species composition of the rumen microflora, rumen pH) and to structural and chemical characteristics of the plant material.

The proportions in which the products of digestion are represented may affect the efficiency with which a feed is utilized for a particular production process, e.g. fattening or lactation (BLAXTER, 1962, Chs. 12 and 13). Herbage variety and stage of maturity of the plant tissue lead to differences in the relative proportions of volatile fatty acids produced by digestion (BLAXTER, 1962, Ch. 11; MICHELL, 1974; HAWKE, 1963). However, there is some evidence that the animal may adapt to changes in the volatile fatty acid proportions over a period of about fifteen days

so that in the long term they may be used with equal efficiency (BULL, REID & JOHNSON, 1970).

These factors affecting the nutritive value of herbage have been reviewed by RAYMOND (1966, 1969), COOPER (1973) and ULYATT (1973). They show that digestibility and rate of digestion play a large part in determining the nutritive value of plant material. This thesis is concerned mainly with pasture digestibility and in particular the distribution of digestible dry matter in grass swards. It is important to relate herbage digestibility to sward structure so that the nature of the material ingested by an animal can be considered.

Other factors affecting intake of nutrients have not been examined although it is recognised that a model of the pasture component of grazing systems should be built in a form that will accommodate factors regulating intake. Indeed ULYATT (1973) concludes that at least 50% of the variation in feeding value between herbages is attributable to differences in voluntary intake; some of the authors he reviewed put the value even higher than this.

3.2.2 DIGESTIBILITY AND THE AVAILABILITY OF DIGESTIBLE DRY MATTER IN SWARDS

The digestibility of a feed can be expressed on a dry matter or organic matter basis; the concept of digestibility can also be applied to a particular chemical constituent.

$$\text{Digestibility} = \frac{\text{Weight of feed substance} - \text{Weight of undigested residue}}{\text{Weight of feed substance}} \times 100$$

The true digestibility of a material is the percentage weight of that material which passes through the gut wall into the animal's body. Analyses for digestibility *in vivo* or *in vitro* do not measure

the true digestibility of a material but give approximations to it: the 'apparent digestibility' *in vivo* or the 'apparent digestibility' *in vitro*. Apparent digestibility is the parameter used in this thesis. It differs from true digestibility in that the measured "undigested residue" includes undigested bacterial material (*in vivo* and *in vitro*) and mucus, salts and bile residues (*in vivo*).

The nutritive value of pasture has commonly been measured in terms of whole plant digestibility but this gives an imprecise understanding of the availability of digestible material to grazing animals. Measurements of whole plant digestibility are useful in swards cut for conservation or zero-grazing, but in grazed pastures only small portions of the plant are removed at any one time, even when heavily stocked (HODGSON, 1974). Furthermore, at least in a grazing situation, the generalisation that pasture digestibility declines with age (for references see p. 64) is not helpful and could be misleading.

In this thesis, therefore, the nutritional content of herbage is analysed in terms of the growth, maturation and senescence of the individual leaf, sheath and stem. Three areas of interest are relevant to the analysis:

(1) the biochemical basis behind differences in digestibility;

(2) the tissue changes that constitute maturation and senescence.

(3) the progress of morphological development of leaves and stem on a tiller and their spatial disposition.

The 2nd Section of the Literature Review has been developed along these three lines.

3.2.3 CELL STRUCTURE AND DEVELOPMENT IN RELATION TO NUTRITIONAL CONTENT AND DIGESTIBILITY

3.2.3.1 CHEMICAL COMPONENTS OF PLANT CELLS

A large body of information has been built up on the structural composition of plant tissues and on the digestibilities of individual molecular components. Recent reviews have been published in the Chemistry and Biochemistry of Herbage (ed. BUTLER & BAILEY, 1973) on the non-structural carbohydrates (SMITH, 1973); the structural carbohydrates (BAILEY, 1973); lignin (HARKIN, 1973) and the mineral content of herbage (BUTLER & JONES, 1973; FLEMING, 1973; and WHITEHEAD, 1966).

Developmental changes within leaf cells from expansion to senescence have been discussed by BRADY (1973), and within tissues of the shoot by JOHNSTON & WAITE (1965).

The chemical components of perennial ryegrass, the percentages in which they occur, and their apparent digestibilities, are tabulated in Appendix 1. As far as possible the information has been gathered from studies with the variety S24.

Chemical components of plant cells can be considered in two categories in relation to nutrient intake:

(1) Cell Contents, which are completely digestible, and

(2) Cell Wall Constituents, which vary considerably in digestibility.

3.2.3.2 CELL CONTENTS

The major substances by dry weight in cell cytoplasm are protein-lipid complexes, which make up cell organelles and enzyme systems, and - in certain tissues - storage carbohydrates. Simple sugars, amino acids, mineral ions and vitamins are also

present but each constitute only 2 to 5% of the cell contents.

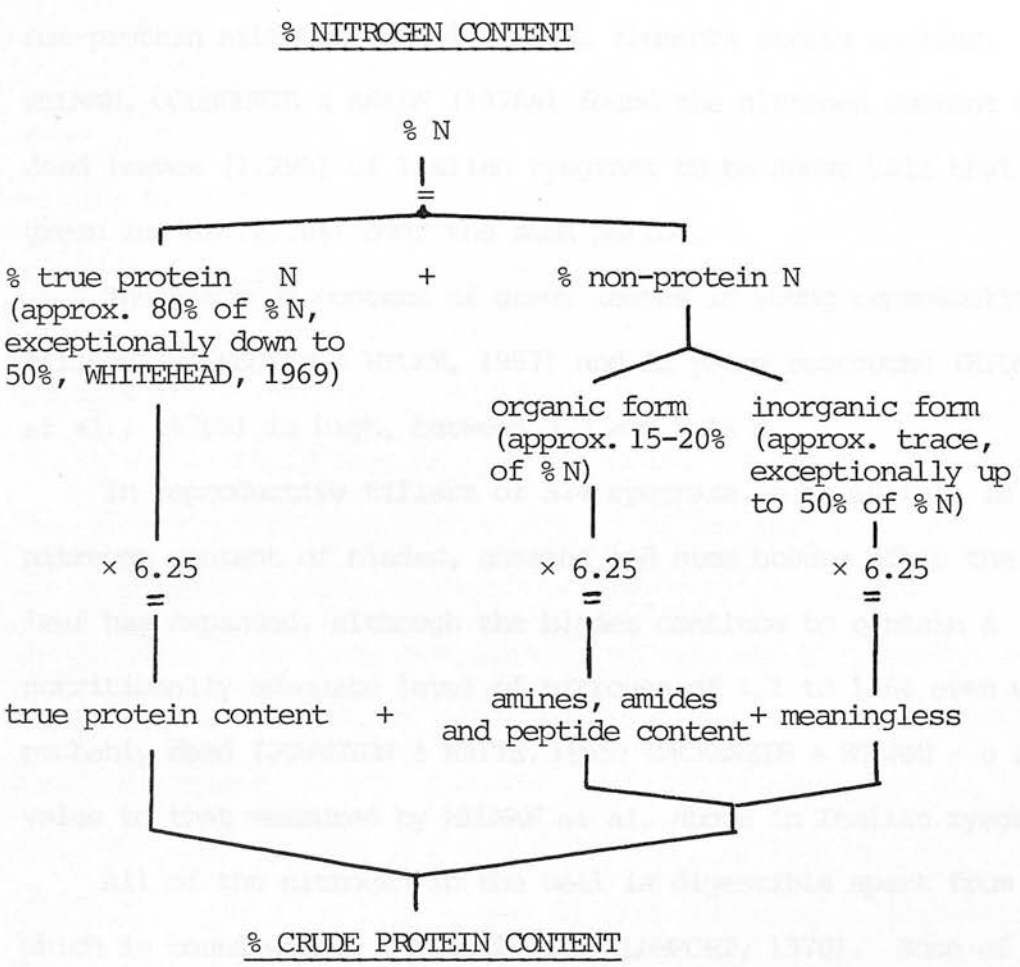
Dry weight per cell increases as more organelles are formed (BRADY, 1973), reaching a maximum some time after full leaf expansion (DEINUM & DIRVEN, 1971, *Zea Mays*). Total cell contents in Italian ryegrass were found to stay at much the same level in green leaves, from 67% in immature blades and sheaths to 65% in mature blades and 60% in mature sheaths. Contents then declined considerably to 50% in senescent leaves (HARTLEY, 1972). In S24 ryegrass cell contents ranged on average from 66% in young leafy plants to 49% in mature stem (MACKENZIE & WYLAM, 1957).

From the nutritional point of view the important changes that take place in the cytoplasm are in nitrogen content, fructosan content and in some of the mineral elements present.

3.2.3.2a Nitrogen content

Nitrogen occurs in the plant principally in proteins and amino acids, and as nitrate. It is taken up from the soil as nitrate or ammonia (DEINUM, 1966) and reduced, using energy derived from water-soluble carbohydrates, before the plant can use it. This accounts for the inverse relationship between the nitrogen and the water-soluble carbohydrate contents of plant tissue. As nitrogen fertilizer rates are increased, the percentage nitrogen content of the plant increases; at high fertilizer levels the increase takes place mainly in the non-protein nitrogen fraction whilst water-soluble carbohydrate content becomes very low (RAHMAN, McDONALD & SIMPSON, 1960; HERLIHY, 1973).

The nitrogen content of plant tissue is published either as % nitrogen (% N) or as crude protein:



The percentage nitrogen content of young leaf cells as they emerge is high (45% protein content in wheat) and even higher in the unemerged leaves; by maturity the protein content of wheat leaves has fallen to a fairly constant level of 39% (WILLIAMS & RIJVEN, 1965). When nitrogen is available in the soil it is taken up very quickly by the plant and may accumulate in large quantities (WILMAN, 1965; BEHAEGE & CARLIER, 1974) particularly, presumably, in the growing leaves, since senescent leaves are exporting much of their nitrogen (WILLIAMS, 1955). The protein-nitrogen content of a cell remains fairly constant in mature leaves after expansion has ceased (BRADY, 1973). Different sets of enzymes are formed and broken down as the leaf progresses from an anabolic to a catabolic phase of development (HEDLEY & STODDART, 1972); it is only

in senescent leaves that net protein content declines. Export of non-protein nitrogen and of mineral elements starts earlier. WILMAN, OJUEDERIE & ASARE (1976a) found the nitrogen content of dead leaves (1.29%) of Italian ryegrass to be about half that of green leaves (2.50%) over the same period.

The nitrogen content of green leaves in young reproductive tillers (MACKENZIE & WYLAM, 1957) and in young regrowths (WILMAN *et al.*, 1976a) is high, between 3.3 and 5.1% N.

In reproductive tillers of S24 ryegrass, a rapid fall in nitrogen content of blades, sheaths and stem occurs after the flag leaf has expanded, although the blades continue to contain a nutritionally adequate level of nitrogen of 1.1 to 1.6% even when probably dead (JOHNSTON & WAITE, 1965; MACKENZIE & WYLAM) - a similar value to that measured by WILMAN *et al.* above in Italian ryegrass.

All of the nitrogen in the cell is digestible apart from some which is bound within the cell wall (LAMPORT, 1970). Some of the nitrogen is lost in undigested microbial material. The apparent digestibility of nitrogen is therefore usually between 70 and 80% (ARMSTRONG, 1974).

Apparent digestibility of nitrogen, varies with plant tissue from 81% in leafy reproductive S24 ryegrass to 71% when only 20% of the heads have emerged (WAITE, JOHNSTON & ARMSTRONG, 1964) and down to 24% in mature reproductive tillers after head emergence (TILLEY & TERRY, 1969). The proportion of the nitrogen that is in a bound state will increase as the soluble nitrogen content of a cell decreases with age. JARRIGE & MINSON (1964) found that the amount of apparently undigested crude protein remained remarkably constant at 4.5% of the total dry matter of S24

ryegrass throughout the whole of the first cycle of growth - even though total crude protein content fell from 22% down to 8%. It seems likely that the observed apparent digestibility of nitrogen is made up of two parts:

(1) completely digestible soluble N

(2) relatively indigestible bound cell-wall N;

and that bound nitrogen remains fairly constant whilst the soluble nitrogen content of the cell is decreasing with age.

MOIR & HARRIS (1962) have shown that the bacterial count in the rumen of the sheep is highly correlated with the % of nitrogen in the diet. Intake is reduced when %N content is reduced below about 1%, suggesting that rumen microbial activity is limited by a nitrogen content of less than 1%. The recommended %N in the diet for a 500 Kg dairy cow yielding 15 Kg milk per day is 1.4% (WHITEHEAD, 1966), and for a ewe in late pregnancy 1.7% (calculated from tables given by the Meat and Livestock Commission handbook "Feeding the Ewe", and by the Agricultural Development and Advisory Service Advisory Paper No. 11).

When the availability of nitrogen in the soil is low, or when growth has been very rapid (as in primary cuts for conservation in some varieties and in some years: MILES, WALTERS & EVANS, 1969; DENT & ALDRICH, 1970), the nitrogen content of herbage may fall below the requirements of both the rumen micro-organisms and the animal. Under fairly intensive grazing conditions, on the other hand, grass supplies more protein than is necessary even at the highest levels of production (JONES, 1972) - provided that the animal can ingest sufficient dry matter. Nitrogen surplus to rumen micro-organism requirement is wasted, and high levels of nitrate can be toxic (BEHAEGE & CARLIER, 1974).

3.2.3.2b Fructosan content

Fructosans act as storage polysaccharides in temperate Festucoid grasses. They accumulate or disappear from leaf sheaths (EAGLES, 1967a) and stems (MACKENZIE & WYLAM, 1957; SMITH, 1973), particularly in the basal portions. Fructosan content of stem increases considerably throughout the year from 2 to 21%; in leaf blades it remains at 0 - 2% until autumn when it increases up to 6% (MACKENZIE & WYLAM, 1957 : S24).

Fructosans are completely digestible; therefore factors leading to changes in fructosan content would be expected to affect tissue digestibility. Increase in net assimilation (at higher light intensities, lower temperatures) was found to result in increased water-soluble carbohydrate content (DEINUM, 1966), most of which would be due to fructosan. Increase in growth rate, on the other hand, led to lower fructosan reserves (at higher temperatures, heavier nitrogen fertilizer levels : WAITE (1970); and during stem elongation in some grass species other than ryegrass : WAITE & BOYD (1953a)).

3.2.3.2c Mineral content

Mineral elements essential in animal nutrition are N, P, K, Ca, Mg, S, Na and Cl, and trace quantities of Fe, Cu, Mn, Mb, Co, Zn, I and Se (FLEMING, 1973).

The mineral composition of herbage has been reviewed by FLEMING (1973) in relation to distribution between plant parts, stage of maturity and season of the year. The availability of the minerals to the ruminant may be reduced if they are bound within complex organic molecules which are not susceptible to digestion e.g. magnesium (JONES, 1972).

Distribution within the plant varies partly in relation to the mobility of the element (LONERAGAN, 1973) and partly in relation to the plant part. N, P, K and Mn are highly mobile and appear in higher concentrations in growing tissues than in older leaves, from which they are recirculated (WILLIAMS, 1955). The trace elements and calcium are immobile (WILLIAMS, 1963) so deficiencies of these elements are first observed in the younger leaves. The mobility of other elements is intermediate.

FLEMING (1963) and PRITCHARD, PIGDEN & FOLKINS (1964) found that the % concentration of Ca, Mg and N was generally two to three times greater in leaves than in stem, and that of potassium and phosphorus was slightly higher.

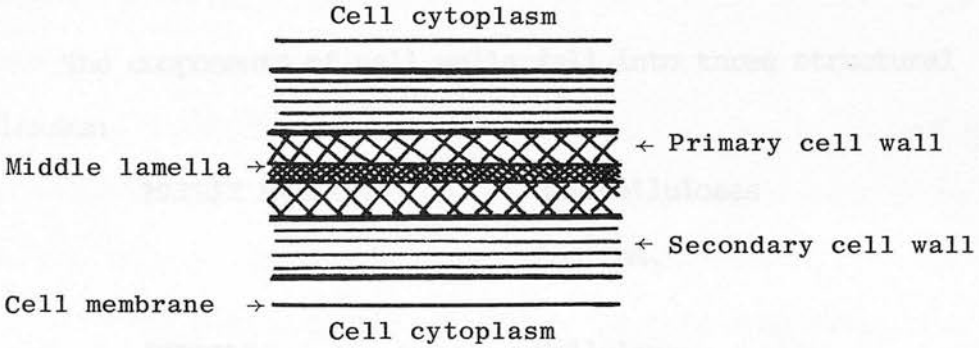
WILLIAMS (1963) points out that "grazing management can considerably affect the minor-element content of pastures, probably mostly by changing the leaf/stem ratio and the relative proportions of young and old leaf material available for grazing". This statement can be extended to include the major elements as well.

3.2.3.3. CELL WALL

3.2.3.3a STRUCTURE AND CHEMICAL COMPOSITION

Accounts of cell wall structure have been written by ESAU (1965) and BAILEY (1973).

When a plant cell is first formed, the protoplasm is enclosed by a protein-lipid membrane only. As the cell expands a primary cell wall is built up outside the membrane from substances secreted from within the cell. Between adjacent cells a layer called the middle lamella is formed. After cell expansion stops a secondary cell wall is laid down between the primary wall and the cell membrane. Electron micrographs show the layered structure of the mature cell wall (ESAU, 1965), represented diagramatically as follows:



The primary cell wall is mainly composed of a hemicellulose matrix (35 - 50%) and an initially irregular but increasingly parallel network of cellulose fibrils (25 - 30%) (SETTERFIELD & BAYLEY, 1961; ROELOFSEN, 1965). Also present are pectins (10 - 20%), glycoprotein (3 - 10%) and lipid (2 - 7%). Tissues such as the mesophyll and palisade layers of leaf tissue only have a primary cell wall.

The middle lamella is made up almost entirely of an amorphous matrix of pectic material. It cements the cells together and is also able to hold a large quantity of water (ESAU, 1965).

The secondary wall is laid down after cell expansion has almost stopped. It contains a greater proportion of cellulose to hemicellulose than in the primary wall (see BAILEY, 1973). Cellulose fibres tend to lie parallel to the wall, forming a lattice. Interlacing with this lattice, in heavily lignified cell walls, is a lattice of lignin (BAILEY, 1954). Lignification tends to take place after the cellulose network has developed, and occurs in both primary and secondary walls (WARDROP & BLAND, 1959). Secondary walls are formed chiefly in vascular and strengthening tissue (ESAU, 1965).

The components of cell walls fall into three structural classes:

MATRIX MATERIAL	Hemicelluloses
	Pectins.
FIBRILS	Cellulose
	A little Hemicellulose
	Glycoprotein (Extensin)
IMPREGNATING OR	Lignin
ENCRUSTING MATERIAL	Silica
	Waxes.

Cellulose is a long linear polymer of glucose units forming a microfibril. Microfibrils are held together by hydrogen bonds to give the fibres seen in electron micrographs.

Hemicellulose is a group name for the matrix polysaccharides, apart from the pectins. The main hemicellulose - xylan - is a polymer of the pentose sugar xylose. Attached to the chain are other sugars including arabinose, glucuronic acid and galactose. Hemicelluloses are, therefore, highly branched (unlike cellulose) and contain a number of different types of linkage with respect to enzyme attack.

Pectic substances are related to hemicellulose but have different solubilities. They are a group of polysaccharides based on polygalacturonic acids, often with calcium and magnesium as side groups. Associated with pectins are galactans, arabans and galactoarabans.

The presence of a glycoprotein, extensin, has not been conclusively demonstrated (BAILEY, 1973) but it is thought to be involved in the expansion of the cell wall as cell volume increases (LAMPORT, 1970). In cell wall analyses it is probably included in the hemicellulose fraction since it appears to be made up of glycans plus hydroxyproline-rich protein.

Lignin, silica and waxes tend to be laid down later than the polysaccharides and so perhaps encrust and impregnate the wall.

Lignin is still difficult to isolate and define. It is a polymer based on three closely related phenyl alcohols (p-coumaryl, coniferyl and sinapyl alcohols). Irregular but very strong interconnections take place between the monomer units in the form of carbon-carbon bonds and ether linkages. Further bonds are made between lignin and the structural carbohydrates, some of them also very strong (HARKIN, 1973).

Silica appears to have a structural role in grasses, being found mainly in the cell wall of all epidermal, vascular and fibrous tissue (JONES, MILNE & WADHAM, 1963).

3.2.3.3b DIGESTIBILITY OF THE CELL WALL

The digestibility of the cell wall is always less than the sum of the parts. Cellulose and hemicellulose can be completely broken down by rumen microbial enzymes but when contained within the cell wall their accessibility to enzymes is chemically and physically impeded. There are two main reasons: the first involves cellulose alone; the second concerns the bonding of lignin to other structural molecules.

(i) THE EFFECT OF CELLULOSE ON DIGESTIBILITY

Deposition of cellulose seems to take place in two main stages (MARX-FIGINI, 1966). In the first stage short cellulose microfibrils are built apparently in association with the formation of the primary cell wall, in which an initially irregular network of fibrils has been observed (SETTERFIELD & BAYLEY, 1961). In the second stage much longer, regular, cellulose polymers are formed in much larger quantities. They appear to be laid down in longitudinal crystalline bundles in the secondary cell wall. Since crystalline cellulose is not easily attacked by enzymes (YOUATT, 1958), the increase in cellulose crystallinity with deposition of the secondary wall (SETTERFIELD & BAYLEY, 1961) and with time of storage, therefore possibly with age (STERLING & SHIMAZU, 1961) would lead to cellulose being more slowly digested. This may partly explain the strong correlation that ALLINSON & OSBOURN (1970) found between voluntary food intake and the percentage of the total digesta that was derived from

cellulose. JONES & BAILEY (1974) also found that voluntary intake and cellulose content were correlated ($r = -0.76$, $P < 0.001$). However, correlation between voluntary food intake and the amount of cell wall left undigested after treatment with an enzyme preparation containing celluloses, hemicelluloses and proteases, was greater ($r = -0.88$, $P < 0.001$).

(ii) THE EFFECT OF LIGNIN-CARBOHYDRATE COMPLEXES ON DIGESTIBILITY

The major agent in reducing cell-wall digestibility is lignin. There is a generally held view that lignin reduces the digestibility of the cell wall both by physically encrusting the structural molecules (FORD, 1973; KAMSTRA, MOXON & BENTLEY, 1958), and by strong chemical bonds with the polysaccharides.

As lignin is laid down it forms high molecular weight complexes with the structural carbohydrates, in which the proportion of lignin to carbohydrate remains constant (MORRISON, 1974c). MORRISON postulated three types of bonding between phenolic acids on the lignin side, and mainly glucose (cellulose) and xylose (xylan hemicellulose) on the carbohydrate side. About half of the complexes appeared to be with cellulose and the other half with hemicellulose. He found that there was a difference in the structure of the cell wall of the leaf blade compared with the leaf sheath and stem (MORRISON, 1974b). Coincident with these dissimilarities in cell wall structure are the falls in digestibility with tissue age in leaves and stems. JOHNSTON & WAITE (1965) found that, at least in reproductive tillers, the leaf sheath declined in digestibility in a similar pattern to that of the stem but somewhat less so to that of the blade.

Complexes between lignin and hemicellulose

The observations of MORRISON (1974a and 1974b) and WAITE, JOHNSTON & ARMSTRONG (1964) together suggest that a link particularly important in lowering digestibility is one which occurs between lignin and xylan hemicellulose. Thus, while S23 ryegrass matured from a young leafy stage through to seed ripening, the digestibilities of hemicellulose and pectin declined most. The digestibility of hemicellulose fell from 91% to 57% and the digestibility of pectin fell from 72% to 36%. The digestibility of cellulose, on the other hand, fell rather less (92% to 73%). The large decrease in pectin digestibility fits in with LAMPORT's statement (1970) that some cell wall components are unstable after formation, notably the pectic substances.

Further evidence links differences in cell wall digestibility within the same plant with changes in the hemicellulose-lignin complex of plant parts as they age. HARTLEY, HALL & JONES (1970) show that on the lignin side of the complex, ferulic and p-coumaric acids are involved in ester linkages with the carbohydrates. (Both phenyl acids are precursors in the formation of the phenyl alcohol units of lignin (HARKIN, 1973)). It is striking that

a) the proportion of ester linkages that involve ferulic and p-coumaric acids,

b) the ratio of ferulic to p-coumaric acid

and c) cell wall digestibility

(HARTLEY, 1972) all vary between tissues in the same manner. Indeed the last two factors are highly correlated ($r = 0.98$, $P < 0.001$).

In addition, WAITE, JOHNSTON & ARMSTRONG (1964) have shown that lignin is initially partially digestible in young tissue (42 - 23% depending on species). WARDROP & BLAND (1959), using spectroscopy, suggest that at first some of the side chains in lignin are free.

It is possible to inter-relate the above observations on hemicellulose - lignin and lignin by making two speculations. Firstly, that the ferulic acid linkage is susceptible to enzyme attack, and secondly that two-thirds of such linkages disappear during senescence to be replaced by even stronger, indigestible, bonds. This process would lead to the observations stated earlier: (a) a 20% drop in the percentage of ester linkages involving ferulic and p-coumaric acids, (b) a fall from 30% to 10% in the ratio of ferulic acid to coumaric acid, and (c) a drop in digestibility if the ferulic acid - ester link had been allowing the digestion of some lignin.

Complexes between lignin and cellulose

The investigations of those people who concentrated on cellulose have emphasised the relationship between lignin and cellulose in reducing cell wall digestibility. ALLINSON & OSBOURN (1970) found that dry matter digestibility changes were closely associated with cellulose digestibility changes. The decline in cellulose digestibility was correlated with the appearance of a lignin fraction in the cell wall. WILKINS (1972) showed that the amount of indigestible cellulose was highly correlated with lignin content in a number of species ($r = 0.96$, $P < 0.001$). HAN, LEE & ANDERSON (1975) working with ryegrass straw found that lignin and cellulose were both

significantly correlated with digestibility. However, multicorrelation analysis showed that in the lignin - cellulose complex it was mainly lignin which influenced the digestibility whereas cellulose was non-significant.

In some conserved grass feeds some of the lignin-carbohydrate bonds are broken, making more material available to the animal (HARKIN, 1973). Fibres in hay swell when treated with alkali and alkali-labile bonds break. In silage the fatty acids produced can lower the pH to a level at which some acid-labile bonds are broken. Processing of dried grass pellets and milling of laboratory samples could disrupt some of the encrusted lignin.

(iii) THE EFFECTS OF SILICA AND WAXES ON DIGESTIBILITY

There is some controversy over the influence of silica on digestibility. VAN SOEST & JONES (1968) found that in Reed Canary grass digestibility fell three units for every one unit increase in silica content. When this relationship was incorporated into predictive equations for dry matter digestibility of a number of grass species, it overcame about 60% of the discrepancies that they had previously obtained between *in vivo* and predicted dry matter digestibilities. DEINUM & DIRVEN (1971) also reported an apparent association between increasing silica content and decreasing digestibility in an ageing maize leaf. Both these sets of evidence are associative, not causal.

On the other hand, HARTLEY, JONES & HALL (1970), VAN SOEST & JONES (1968) - both using oat plants, and DALY (1976) - using S24 Ryegrass, S37 Cocksfoot and S170 Tall Fescue, found no evidence that increasing silica content in herbage dry matter caused a lower digestibility in their material. HARTLEY *et al.*

and VAN SOEST & JONES both suggest, however, that where there is an association between soluble silica and lowered digestibility this may indicate the existence of unknown soluble inhibitors of polysaccharide digestion in some species. DALY was only able to demonstrate this association when both the amount of soluble silica in the rumen liquor was augmented to quite a high level, and the digestibility of the sample material was quite low (about 50% dry matter digestibility).

There is little published work on the effect of wax on digestibility. HANNA, MONSON & BURTON (1973) showed that the waxes that make up the cuticle of the plant form a strong physical barrier to enzyme attack on epidermal cell walls. WILSON (1976b) has found that the development of the cuticle may be associated with a rapid fall in tissue digestibility.

3.2.3.4 THE EFFECT OF ENVIRONMENT ON DIGESTIBILITY

DEINUM, VAN ES & VAN SOEST (1968) found that the environment affected plant digestibility less than it affected chemical composition, particularly the soluble components (see section 3.2.3.2b on fructosan content). Increasing light intensity had a small positive influence on digestibility; warmer temperatures had a rather large negative influence (see also WILSON & FORD, 1971): and higher nitrogen fertilizer rates had a non-significant but positive trend (see also MINSON, RAYMOND & HARRIS, 1960; LAMPETER, MATTHIES & TCHAPTCHET, 1973). HARKESS, FRAME & HUNT (1971), however, found that increasing the application of nitrogen from 25 to 125 Kg ha^{-1} decreased the digestibility of pure S24 ryegrass swards by 3 to 4 units. The decrease in whole plant digestibility was greater at later harvests and, from the results of WILMAN, KOOCHEKI & LWOGA (1976b), is likely to have been due to an increased proportion of mature stem to leaf.

Cell wall contents, comprising 40 - 60% of the plant dry matter (see Appendix 1), showed no significant response to temperature, light or nitrogen fertilizer in terms of their percentage contributions to the dry matter (DEINUM *et al.*, 1968). This was contra-indicated in a later paper by DEINUM & DIRVEN (1971) in which increasing temperature led to an increase in cell wall constituents (including an increase in lignin) and a decrease in its digestibility; between $15^{o}/10^{o}C$ and $20^{o}/15^{o}C$ the digestibility of blade and sheath fell by about 5 units.

Thus, although there may be changes in various cell components in response to the environment, it appears that tissue digestibility is altered to a lesser extent. This is to be expected since variation in one cell constituent may be counterbalanced by variations in others.

3.2.3.5 RATE OF PASSAGE OF FOOD THROUGH THE RUMEN

The cell wall is of great importance in determining the nutritive value of grass. The sheer bulk of the indigestible portion reduces the volume of the rumen that can hold digestible material. The remaining potentially digestible part of the feed is, *in vivo*, only partially broken down.

The passage of material out of the rumen into the abomasum is dependent upon a reduction in particle size. The more fibrous the material (i.e. the greater the proportion of lignified, vascular and strengthening tissues), the longer will it take before mastication and digestion have broken down the ingested material into small enough particles. The rate at which material passes out of the rumen limits the rate at which more material can be taken in (BALCH & CAMPLING, 1962). This helps to explain why there is a stronger correlation between intake and percentage cell wall content (DEINUM, 1974; JONES & BAILEY, 1974), or intake and percentage cellulose content (ALLINSON & OSBOURN, 1970) than between intake and digestibility *per se*, since digestibility has no time dimension.

Before material does pass into the abomasum it should, ideally, have been in the rumen a sufficient length of time for the potentially digestible cell wall material to have been broken down by microbial enzymes. The advisability of a certain amount of fibre in offered feeds, and the importance of fibre length in pelleted feeds to the rate of passage, are apparent.

Some 'potentially' digestible material would still remain undigested however long it remained in the rumen, due to its close association with indigestible substances.

The amount of ingested herbage rendered soluble per unit time is, therefore, a function of rate of passage and of digestibility. HODGSON (1977) presents evidence from several sources to show that intake increases linearly with digestibility in growing or lactating animals. The relationship described by BLAXTER *et al.* (1961) and BLAXTER & WILSON (1962), in which intake increases more slowly above 65% digestibility, refers to mature non-productive animals.

3.2.3.6 SUMMARY OF THE RELATION OF PLANT CELL STRUCTURE TO PASTURE NUTRITIVE VALUE

The digestibility of a tissue is determined partly by the proportion of the dry weight that is attributable to cell contents, and partly by the structure of the cell walls and their susceptibility to enzyme attack.

Cell contents constitute 66 to 49% of the dry weight and are completely digestible. The changes of nutritional importance that take place in the cytoplasm, with season or with tissue age, are largely in the fructosan or nitrogen content; mineral deficiencies or toxicities may also occur.

The cell wall is built in layers. The primary cell wall is built during cell expansion, mainly from hemicellulose, cellulose and some glycoprotein. The structure is necessarily relatively labile to allow for expansion growth, and the wall is quite highly digestible. The secondary wall is laid down, in strengthening and conducting tissues in particular, as cell growth slows down. It is a much more rigid, ordered structure of hemicellulose and cellulose interwoven or encrusted with lignin. Many lignin and

lignin-polysaccharide bonds are not susceptible to enzyme attack and the digestibility of the mature cell wall can be very low. Not all cell tissues have secondary cell walls; such tissues are more highly digestible.

Although the structure of the cell wall and its susceptibility to physical and enzymic breakdown is not yet fully understood, it is clear that cell wall digestibility declines as tissues grow older and that it varies with species. Both considerations are important in grassland management and utilization.

The nutritive value of pasture is determined not only by its digestibility and nutritional content but also by factors affecting the amount of it that is ingested by an animal. It has been established that the rate of cell wall digestion is of great importance in limiting voluntary intake. Rate of digestion is, to a large extent, dependent on the physical and chemical structure of the cell wall, but there is also an absolute requirement by the rumen micro-organisms for nitrogen and certain minerals.

3.2.4 PLANT PARTS : THEIR STRUCTURE AND DIGESTIBILITY

Very few investigations have been carried out into the digestibilities of successively older leaves on a tiller (DEINUM & DIRVEN, 1971: *Zea Mays*; HAGGAR & AHMED, 1971: *Andropogon gayanus*; HARTLEY, 1972: *Lolium multiflorum*; WILSON, 1976a: *Panicum maximum*). Few of these studies can be directly extrapolated to vegetative tillers in temperate grass species. There is more information available on the decline in digestibility with age of stem tissue (PRITCHARD, FOLKINS & PIGDEN, 1963 ; TERRY & TILLEY, 1964 ; JOHNSTON & WAITE, 1965).

Water soluble carbohydrate content varies between plant parts and changes with age (SMITH, 1973). Measurements have been made of the soluble carbohydrate content in different parts of the plant during periods of the year for S24 and S23 perennial ryegrass by WAITE & BOYD (1953a, 1953b), MACKENZIE & WYLAM (1957), JARRIGE & MINSON (1964) and TERRY & TILLEY (1964).

Changes in crude protein content with tissue and with age have been discussed in Section 3.2.3.2a. HAGGAR & AHMED (1971) followed the changes in crude protein content of leaf laminae and stem (plus sheath) as they age in a tropical grass *Andropogon gayanus*.

JONES (1972) and FLEMING (1973) conclude that mineral elements in different plant parts and at different stages of maturity can vary in digestibility when bound within organic molecules. The distribution of minerals in different parts of the plant has been referred to in Section 3.2.3.2c.

The structural carbohydrate content of different parts of the plant and the changes throughout the year are reviewed by

BAILEY (1973). JARRIGE (1963) found that the percentages of cellulose and xylan hemicellulose are less in leaf blade than in stem or than in sheath in perennial ryegrass at the time of flowering; while KRUEGER, HAMILTON, SCHOLL & BAUMGARDT (1969) showed that the amounts of acid-detergent fibre, lignin and nitrogen varied in different parts of the plant. Changes in composition of the cell wall and the digestibilities of its constituents with age have been observed by WAITE, JOHNSTON & ARMSTRONG (1962) and MORRISON (1974a), among others.

The only tissues found remaining intact following *in vitro* digestion in several grass species were the cuticle, trichomes, xylem, fibres and bundle sheaths (HANNA, MONSON & BURTON, 1973). After a 48-hour digestion some non-lignified cells attached to schlerenchyma were also undigested (WILKINS, 1969). The development of lignification in leaves, sheaths and stem of grasses has been examined by JOHNSTON & WAITE (1965) in S24 perennial ryegrass and S37 cocksfoot, and in the stems of a number of grass species by STEPPLER (1951). The development of the cuticle in the blade and the sheath of an annual grass, *Panicum maximum*, has been measured by WILSON (1976b).

3.2.4.1 LEAF BLADE

The observations of JOHNSTON & WAITE (1965) suggest the course of structural change that takes place within an individual leaf. At first, only the wood vessels of the vascular bundles are lignified. When the leaf blade is mature, lignification has extended to all fibrous tissue and no further structural change is visible until the leaf starts losing its colour and senescing.

The thin-walled chloroplastic tissue then collapses leaving a skeleton of epidermis, vascular bundles and partially lignified fibres.

The percentage of total water-soluble carbohydrates may not change much as leaves age. The actual changes taking place are not known but informed guesses can be made. Thus from the work of MACKENZIE & WYLAM (1957) and WAITE & BOYD (1953b) it might be expected that total hexoses remain constant at 1 - 2%; sucrose would increase or decrease between 2 and 6% with the metabolic activities of photosynthesis, translocation and anabolism; and fructose would tend to increase with leaf age from about 0% in young leaves to 3 or 4% in mature leaves and to as much as 12% during seed setting. The average water-soluble carbohydrate content of leaf blades of all ages was measured by TERRY & TILLEY (1964) as about 9%, rising to 13% during early stem elongation.

The nitrogen content of young leaves can be very high but by the time the leaf is dead up to 95% of the nitrogen has been transported out of the leaf (WILLIAMS, 1955). The same is true for potassium and phosphorus. Calcium and iron, on the other hand, tend to increase with leaf age, never decrease, while other elements lie somewhere between the two extremes of mobility (LONERAGAN, 1973).

Crude protein content of expanded green leaf in *Andropogon gayanus* was only a little lower than that of emerging leaf (approx. 1%) but fell twice as fast between full leaf expansion and senescence (HAGGAR & AHMED, 1971). Similar changes in crude protein content were measured by I. DAVIES (1969) in S24 ryegrass. % Crude protein of the emerging leaves was about 15%.

Structural carbohydrate content of the cell increases until leaf elongation is complete, then drops again as maximum leaf weight is attained. Thereafter, in tall fescue, for example, the percentage of structural carbohydrates in the cell appears to remain relatively constant even though leaf digestibility is declining (DEINUM & DIRVEN, 1971). In Italian ryegrass, however, changes in the percentages of the structural carbohydrates did occur (HARTLEY, 1972). As leaves grew older, cell wall contents increased slightly from 33% in young blades plus sheaths, to 35% in mature blades. This was accompanied by an increase in lignin and silica. Cell wall content was 5% greater in mature sheaths than in mature blades, apparently owing to a greater amount of hemicellulose; lignin content was also slightly greater. Between maturity and senescence the lignin content of blade plus sheath doubled and cell wall content increased considerably by 10 to 15%. This time the increase was apparently due to cellulose.

WILKINS (1972) has examined the potential digestibility of cellulose in blades and sheaths and found that it was greater in the blade.

The differences and changes in structural carbohydrate content and digestibilities described above suggest that digestibility of leaf blade may decline only slowly as the leaf matures, but faster as it senesces. This has been confirmed in *Andropogon gayanus* by HAGGAR & AHMED (1971). The sheath appears likely to decline faster in digestibility than the blade.

3.2.4.2 LEAF SHEATH

The structure of sheaths is similar to that of blades but some important differences do occur in connection with the supporting role of the sheath (JOHNSTON & WAITE, 1965). The caps of cells over the vascular bundles are larger and thicker; in between the veins are thin-walled parenchyma cells that collapse fairly early on. Further similarities to the stem also occur with respect to silica content (DAVIES, I., 1969), structural carbohydrates (WILKINS, 1969; MORRISON, 1974b) and - in reproductive tillers - nitrogen content (JOHNSTON & WAITE, 1965). The cuticle of the sheath appears to be laid down when the sheath comes into contact with the atmosphere. In an annual (*Panicum maximum*), this occurs soon after blade expansion because of the reproductive growth habit. The cuticle then becomes more strongly developed than that in the blade (WILSON, 1976b). In perennial grasses the sheath would not come into contact with the atmosphere until the 3rd or 4th leaf position.

At cool temperatures, fructosans accumulate in the sheaths reaching up to 13% of the total sheath dry weight in Cocksfoot (EAGLES, 1967b). From the work by JARRIGE & MINSON (1964) on S37 cocksfoot and S24 ryegrass one might expect the percentage to be higher than this in ryegrass. EAGLES (1967a) found that it was to the sheaths in particular that surplus assimilates were translocated, where they were stored as fructosans. The proportions in which the completely digestible fructosan is distributed between young, mature and senescent leaves is not known.

The digestibility of young sheaths might be expected to resemble that of young leaf blades in remaining high until

lignification takes place. It could be even higher than that of the blade because the cuticle is initially thinner and the fructosan content may be greater. At maturity, however, the digestibility could drop below that of the leaf since much of the internal parenchyma, and later the epidermal tissue, collapses (SOPER & MITCHELL, 1955-6). This does not occur in the leaf until senescence (JOHNSTON & WAITE, 1965). Furthermore, the larger amount of vascular interconnection in the sheath (SOPER & MITCHELL, 1955-6) would be expected to influence the digestibility of sheath tissue.

3.2.4.3 STEM

The changes in stem structure with maturity are fully discussed by JOHNSTON & WAITE (1965). Their records, paraphrased, show that up to the time of head emergence there is no lignification; during head emergence a small amount of lignin is laid down in the xylem and pericycle, and the pericycle thickens. By complete head emergence large changes have taken place: the central parenchyma has collapsed, the walls of the vascular tissue and pericycle have become strongly lifnified and thick. Further stem strengthening takes place up to anthesis and thereafter shows little change.

Lignin is laid down to a greater and faster extent in some regions of the stem than in others. The lower internodes of elongating stems are at first more lignified and less digestible than the upper internodes (KRUEGER *et al.*, 1969; JOHNSTON & WAITE, 1965). Lignification of the upper, younger, internodes continues rapidly so that by the time of flowering the position is reversed (PRITCHARD, FOLKINS & PIGDEN, 1963; DAVIES, I., 1969).

The fructosan content of perennial ryegrass stems (plus sheaths) was found to increase from 8% up to 26% during head emergence and thereafter decline (WAITE & BOYD, 1953a).

Crude protein content, although supposedly high in growing tissue (LONERAGAN, 1973) was only 5.5% in unemerged stems. It fell rapidly to 3.1% in the seven days between 50% and 100% head emergence, and declined more slowly thereafter (JOHNSTON & WAITE, 1965). Higher figures for crude protein content in young stem of perennial ryegrass (17.6% - MACKENZIE & WYLAM, 1957) and Italian ryegrass (21% - WILMAN *et al.*, 1976a) have been published, but leaf sheath was included with the stem fraction.

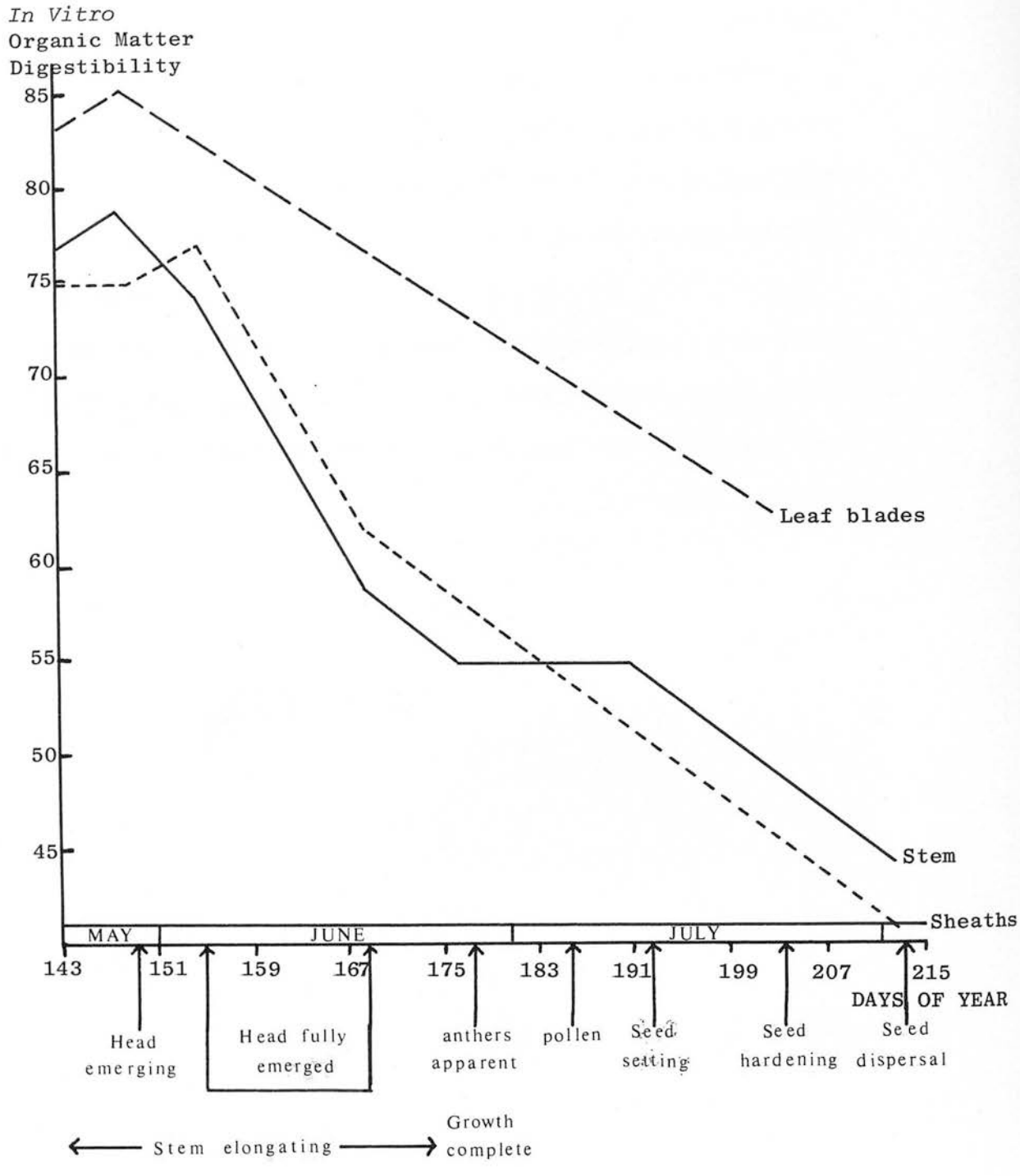


Fig. 3.7 : The *in vitro* organic matter digestibilities of leaf sheath, leaf blade and stem of reproductive S24 perennial ryegrass. Drawn from JOHNSTON & WAITE (1965).

3.2.4.4 DIGESTIBILITY CHANGES IN PARTS OF THE REPRODUCTIVE TILLER

Figure 3.7 relates digestibility changes to reproductive development and has been drawn from the information given by JOHNSTON & WAITE (1965).

The rapid fall in stem digestibility between head emergence and completion of stem elongation corresponds to the great strengthening of the stem structure that takes place at this time.

The further fall in stem digestibility during seed ripening takes place at the same rate as that in the leaf blade (and in the leaf sheath after stem elongation). This common slower rate of decline in digestibility takes place when no visible cell-wall thickening is taking place in any of these plant parts; the digestibility fall is therefore likely to be due solely to changes taking place as cells age.

The rate of change in digestibility of total leaf blades after head emergence is of interest since it is due to ageing of the blade material already present and is not confounded with the addition of new growth of high digestibility. The rate of change of about 1 digestibility unit per week is the average for leaves of all ages; an individual leaf may or may not fall at a linear rate. The rate of fall in digestibility may be different on a reproductive tiller compared with a vegetative one since the physiological demands are so different. However, the only information available in the literature on changes in leaf blade digestibility (with leaf age as opposed to sward age) comes from work with reproductive tillers.

The sheath on a reproductive tiller is performing an exaggeratedly supportive role compared to a sheath on a vegetative tiller; its digestibility changes should not be related to those

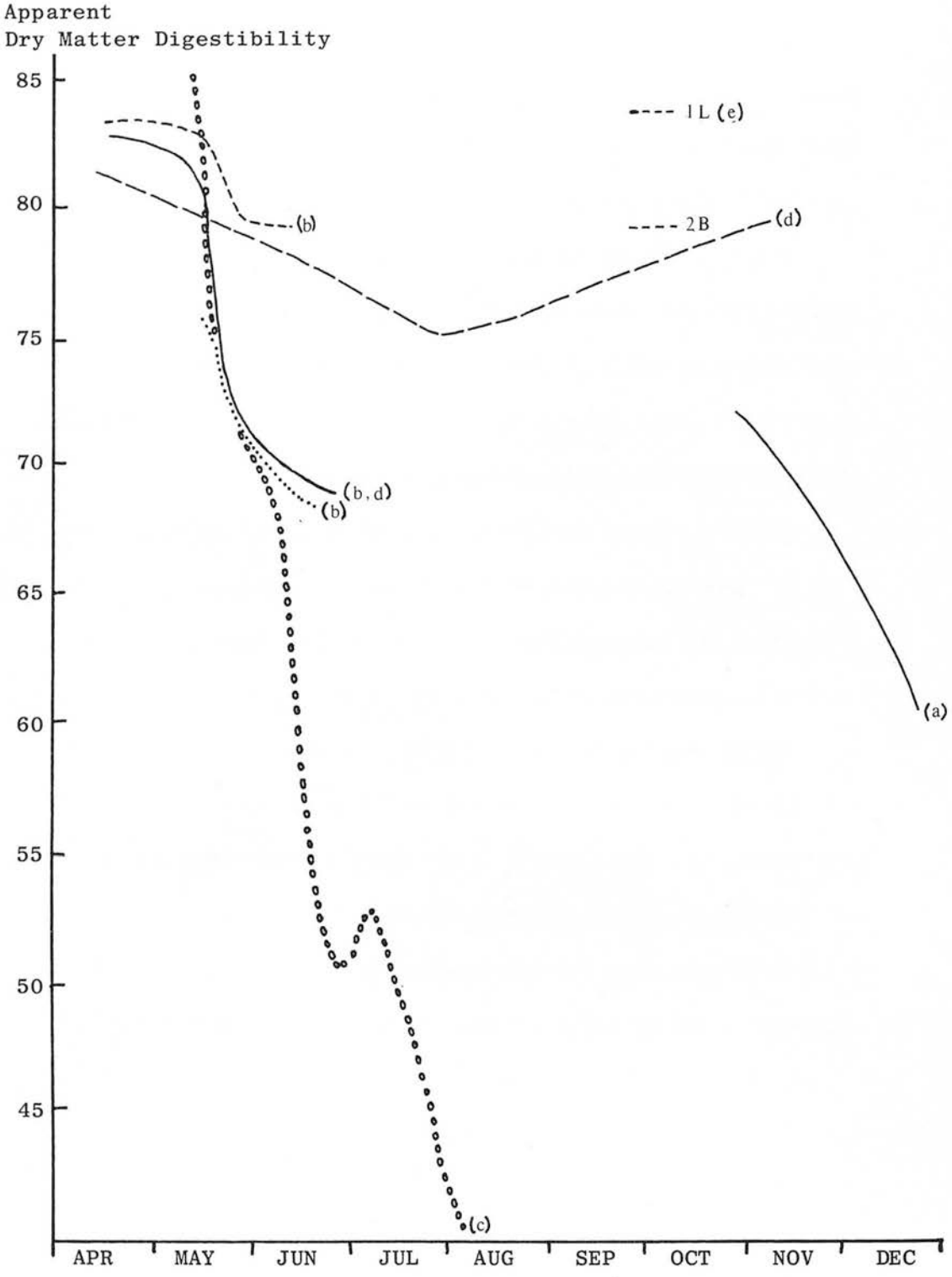
in the vegetative state. It is interesting to note that whilst the sheath of at least the flag leaf is still extending - which it does until head emergence - the digestibility of total sheaths falls as rapidly as that of the stem.

TERRY & TILLEY (1964) have also examined digestibility changes in S24 ryegrass during primary growth. The tillers they examined were all reproductive (pers. comm.). Their results are expressed as dry matter digestibility whereas those of JOHNSTON & WAITE are organic matter digestibilities.

TERRY & TILLEY and JOHNSTON & WAITE found similar rates of fall in stem digestibility during stem elongation (1.27 and 1.07 units per day respectively). Both sets of authors also found a marked temporary lull in stem digestibility change during anthesis.

Their results for leaf blades are also similar (0.21 units per day for green blades and 0.26 for dead leaves: TERRY & TILLEY; 0.14 units per day for all leaf blades: JOHNSTON & WAITE).

During heading, however, TERRY & TILLEY obtained a value of 0.53 units per day for the decline in sheath digestibility whereas JOHNSTON & WAITE found a higher value of 1.07 units per day.



Whole plant

3- or 4-week regrowth

Green leaf

Dead leaf

Stem

3.2.4.5 DIGESTIBILITY OF THE SWARD

The nutritive value of uncut swards has been widely reported as declining with 'maturity' of the plant or with season of the year (e.g. RAYMOND, 1959; HARKESS, 1963; ALDRICH & DENT, 1967; EADIE, 1967). The fall in nutritive value is largely caused by increases in the ratios of stem to leaf and dead material to green (WALTERS, AP GRIFFITH, HUGHES & JONES, 1967).

The relative contributions of the pasture components to overall digestibility are illustrated in Figure 3.8 for S24 ryegrass. In primary cuts the digestibility of the whole plant remains high until ear emergence, when it falls rapidly (TERRY & TILLEY, 1964; DENT & ALDRICH, 1966 and 1968). However, the total green leaf part of the plant continues to remain highly digestible, whereas it has been seen that stem and total sheath digestibility fall fast and to a very low level on reproductive tillers (see Fig. 3.7; JOHNSTON & WAITE, 1965).

Fig. 3.8: Summary of current extent of information about the digestibility of S24 perennial ryegrass and some of its component parts. (Adapted from several sources:

(a) HARKESS (1963) - primary cuts October to December.

(b) TERRY & TILLEY (1964) - Whole plant, green leaf, dead leaf, stem, April to June.

(c) JOHNSTON & WAITE (1965) - Stem, using an approximation that Dry Matter Digestibility = Organic Matter Digestibility - 3.5.

(d) DENT & ALDRICH (1966) - Whole plant primary cuts and whole plant 3 or 4 week regrowths.

(e) I. DAVIES (1969) - Emerged portion of 1st leaf, and 2nd blade, October 5th.)

In monthly cuts, whole plant digestibility is maintained at a relatively high level but it does seem to fall a little in mid-summer (MINSON *et al.*, 1960; HARKESS, 1963; DENT & ALDRICH, 1968). The large fall due to stem maturation is avoided as many stem apices are removed before cell wall thickening takes place. Stem apices just below cutting height, however, could mature quite considerably in the following month and this would lead to a small fall in whole pasture digestibility. It is to be expected that the digestibility of monthly regrowths would be equivalent to that of total green leaves, or possibly be even higher when leaf turnover is slow. The digestibilities of two-month regrowths (MINSON *et al.*, 1960) have not been put on the graph but they fell much further (by about 12 units) in that cut which included the flush of reproductive growth. A fall of about 6 units also occurred over the late summer months relative to the digestibilities of monthly cuts.

The small fall in green leaf digestibility on reproductive tillers by the time of anthesis (TERRY & TILLEY, 1964) has been referred to. (Section 3.2.4.4, p.62). Dead leaf digestibility, though lower than green leaf, is fairly high (TERRY & TILLEY, 1964: S24; MOWAT, CHRISTIE & WINCH, 1965: orchard grass). The digestibility of the 1st leaf in October is 4 units higher than that of the 2nd blade (I. DAVIES, 1969).

3.3 REGROWTH OF GRAZED PASTURE

3.3.1 INTRODUCTION

Sections I and II were concerned with the structure of the sward and the way it is related to the continuing processes of leaf growth and senescence. The consequent range and distribution of units with different digestibilities on a tiller were also examined.

The introduction of a grazing animal to the sward brings about changes in its structure as a consequence of the way in which the animal defoliates that sward.

Section III firstly examines the concept of selection in relation to defoliation and considers the implications it has for the representation of pasture in a grazing model. The effects of defoliation on plant regrowth are then considered.

3.3.2 SELECTIVE GRAZING

The quality of the diet ingested by grazing animals is usually higher than the mean quality of the pasture offered. Grazing is therefore described as 'selective'. Selective grazing can be taken to mean that animals do not graze at random with respect to all the herbage present. Selection can be brought about passively as a result of the non-uniform accessibility of herbage of different qualities; selection may also be positive in that animals may actively reject parts of a pasture or seek out other parts. Attention will be paid here to the simpler situation where animals are grazing from a fairly homogeneous tiller population of a single species.

ARNOLD (1963) put forward the concept that sheep move across a sward grazing it in layers, and select vertically from each tiller, or spot, or patch. The same concept describes the observations made by JOHNSTONE-WALLACE & KENNEDY (1944) on cattle.

In practice the horizontal movement is disturbed by a number of factors which may lead to 'patchiness' in grazing. Firstly there is the flocking behaviour which can vary with breed (SPEDDING, 1965). Secondly there is avoidance of excreta, particularly dung (JOHNSTONE-WALLACE & KENNEDY, 1944); preference between pasture species (ARNOLD, 1963); and a certain distinction between tall and short herbage (see p. 69). Thirdly, there may be a tendency to graze a small area once grazing has started (16 cm × 16 cm: MORRIS, 1967), though it is likely that the degree of patchiness will depend on the homogeneity of the sward, the experience of the animals, fatigue and grazing pressure. For example, HODGSON & OLLERENSHAW (1969) only observed patchy grazing at low grazing pressure.

The frequency with which a particular tiller or clump is grazed depends upon grazing pressure. Grazing of a tiller is at random in time (MORRIS, 1967), but the mean time interval between successive defoliations decreases as grazing pressure increases. The order of magnitude of the interval is six or seven days under heavy sheep stocking (HODGSON, 1966; HODGSON & OLLERENSHAW, 1969; McIVOR & WATKIN, 1973), and is probably not more than twice that under light stocking.

The amount removed per tiller also tends to increase with grazing pressure (MORRIS, 1967; HODGSON & OLLERENSHAW, 1969; McIVOR & WATKIN, 1973). The amount removed is related to bite

size which, in sheep, was found to increase almost linearly with tiller length (ALLDEN & WHITTAKER, 1970). The type of bite will also have an effect between animal species. Sheep nibble and are able to graze more closely to ground level, perhaps covering a smaller area more intensively; they are able to select more precisely (MEYER, LOFGREEN & HULL, 1957). Cattle encompass a larger area with the collecting action of the tongue. They tear the herbage away, rather than bite it (JOHNSTONE-WALLACE & KENNEDY, 1944).

The amount of grass removed has been measured by changes in green leaf length. According to HODGSON (1966) and McIVOR & WATKIN (1973) about 35 - 40% of green leaf length was removed at any one defoliation in a strip-grazing system. DE LUCIA SILVA (1974) measured very much higher figures of 60% removal at a herbage allowance of 5% of metabolic body weight, and 90% removal at 2.5%. Under set-stocking, MORRIS (1967) got a very much lower figure of 19% of total leaf length (green + dead) at low grazing pressure.

All reports confirm that sheep tend to remove the younger, more accessible leaves at the top of the sward or around the sides of a clump (ARNOLD, 1960a, 1963; MORRIS, 1967; GREENWOOD & ARNOLD, 1968; McIVOR & WATKIN, 1973; DE LUCIA SILVA, 1974). Both MORRIS and DE LUCIA SILVA found that the youngest fully expanded leaf (2nd leaf) was grazed most, followed by the emerging leaf and then by the 3rd leaf (half as often as the 2nd leaf). In a reproductive sward the seedheads and first two leaves were eaten most (100%, 90% and 65%), the third leaf was eaten moderately and the lower leaves only a little (20%) (HODGSON, 1966).

Differential removal of the youngest leaves could be accounted for simply because they are at the top of the sward. A certain amount of active selection may also be involved: when the quality of the diet selected by cattle was compared with one clipped to the same height, it was found to be higher (HARDISON, REID, MARTIN & WOOLFOLK, 1954). Active selection is also indicated when animals are not grazing deeper into the sward than the first two leaves or so, given sufficient herbage.

In the case of clover, animals appear to seek it out since they have been observed 'nosing around' for it at the bottom of a sward (ARNOLD, 1960a).

Selection appears to be more pronounced in taller, less dense, mature or reproductive swards (MEYER *et al.*, 1957; ARNOLD, 1960a) where differences in accessibility are more pronounced. There is some evidence that taller tillers are grazed relatively more often than smaller ones (HODGSON, 1966; HODGSON & OLLERENSHAW, 1969; ALLDEN & WHITTAKER, 1970; McIVOR & WATKIN, 1973), but JOHNSTONE-WALLACE & KENNEDY (1944) (with cattle) and ARNOLD (1963) (with sheep) have both observed the smaller leafier tillers being grazed first. ARNOLD points out that the sheep naturally holds its head about 1" from ground level when grazing.

Summary

The younger, more accessible material tends to be grazed first. As grazing pressure increases, the frequency with which a tiller is defoliated increases and there is some evidence to suggest that the amount removed in a bite also increases. The outcome of this is that the sward tends to be grazed in layers from the top as grazing pressure increases. Sheep can be more

selective than cattle. There is greater opportunity for selection, and more evidence of it, in taller, less dense, more mature herbage.

A grazing model must be able to simulate the differential removal of the diet from a sward which has a wide range and distribution of digestible material within it. The morphological units which animals remove (leaves, stems and tillers) require to be represented in the pasture component of the model; their relative spatial distributions, weights and digestibilities should be depicted so that the mechanics of grazing, whether random or selective, can be imposed upon the pasture model.

3.3.3 REGROWTH OF GRASS PLANTS

The partition of assimilates forms the physiological basis of the plant's response to defoliation. Reliable models of pasture growth must, eventually, be based upon the representation of production, partition and utilization of assimilates. The integrated physiology of a grass plant is not yet fully understood.

In the early literature, reports on regrowth after defoliation were largely concerned with changes in net yield. Results were conflicting (see HUOKUNA, 1960; BARNES, 1972) and arose:

(1) partly because defoliation treatments represent an almost infinite range in the combination of weight, quality and frequency of tissue removed;

(2) partly because measurements were made mainly in terms of plant weight changes with little distinction between weight change due to new growth and weight change due to senescence (see MORRIS, 1967; DE LUCIA SILVA, 1974);

(3) basically because the response to the simple act of tissue removal is a highly integrated one involving the whole economy of the plant.

An outline of the distribution of assimilated carbon in intact grass plants will be given first so that the effects of defoliation can be related to it.

3.3.3.1 THE CARBON ECONOMY OF THE INTACT GRASS PLANT

(a) Import of assimilates

Meristematic and expanding leaf cells necessarily import all their substrate requirements since they are enclosed within other leaf tissue. Most of the supply is synthesised in the younger expanded leaf tissue. In *L. perenne* 58% of the assimilate imported

into the terminal meristem (expanding portion of emerging leaf plus younger tissue) comes from the expanded portion of the growing leaf, 25% from the youngest fully expanded leaf and 13% from the next leaf lower down (RYLE & POWELL, 1974). In species with a larger number of leaves per tiller the supply is more evenly contributed to by the first three leaves (20 - 40% from each in *L. temulentum*: RYLE, 1972; 36%, 25% and 20% respectively in uniculm barley: RYLE, BROCKINGTON, POWELL & CROSS, 1973).

In total, the terminal meristematic region receives 18 - 31% of the plants current assimilate (RYLE, 1970a, 1970b; RYLE & POWELL, 1974). Since most dry weight increase probably occurs as leaves are expanding (SILSBURY, 1970), this range supports ROBSON's figure (1973b) of 28% that he calculated for the amount of current assimilate converted into increased leaf weight. Maximum weight of import by the expanding leaf (40 - 55% of its requirements) occurs throughout the major part of a leaf's expansion when it is expanding most rapidly - the rest of the assimilate presumably being supplied by the already exposed portion of the leaf (DOODSON, MANNERS & MYERS, 1964; WILLIAMS, 1964).

8 - 24% of current assimilate is imported by attached tillers, particularly by those with no roots; rooted tillers receive less than 3% (RYLE, 1970b).

(b) Respiration of assimilates

RYLE & POWELL (1974, S24 ryegrass) found that about 25% of current assimilate in the whole plant was respired in the same day that it was formed ("synthetic respiration"), though the actual amount lost by a leaf varied with its age-position on a tiller. ROBSON (1973b) found as much as 45% was respired, half in maintenance respiration and half in the production of new tissue (synthetic respiration).

(c) Export of assimilates

The amount available for export should vary according to the amount respired within the same tissue. The percentages given below for the export of assimilates to the different parts of the plant refer to ^{14}C remaining in the plant after synthetic respiration losses.

Net export from leaf tissue begins as soon as it has stopped growing. Most of the assimilate synthesised in the emerged portion of the growing leaf moves into the expanding region of that leaf and into the rest of the terminal meristem (75% in *L. temulentum*: RYLE & POWELL, 1972; 79% in *L. perenne*: RYLE & POWELL, 1974). The growing leaf appears to be able to produce enough assimilate in the emerged portion to support growth of the expanding portion and yet still export a certain amount to the rest of the plant. DOODSON *et al.* (1964) found that the youngest leaf of wheat translocated nearly 10% of its assimilated carbon into the rest of the plant whilst it was still expanding; in Bahia grass the figure was 16% (BEATY, SAMPAIO, ASHLEY & BROWN, 1974) and in S24 18% (RYLE & POWELL, 1974).

Assimilates exported from the youngest expanded leaf go to the terminal meristem (32%) (RYLE, 1970a), adjacent tillers (20 - 40%) (RYLE, 1970a; RYLE, 1972; RYLE & POWELL, 1974: *L. perenne* and *L. temulentum*) and roots (10 - 25%) (RYLE, 1970a). A negligible amount (3%) goes to the older leaf or leaves. Of the assimilate retained in the leaf, about 70% of it was located in the sheath (RYLE, 1970a: *L. temulentum*) corresponding to EAGLE's observation (1967a) that reserves (fructosans) accumulate in the sheaths.

As leaves grow older, occupying a lower position on the tiller, there is an increasing tendency for their exports to move down into the roots or into adjacent tillers (WILLIAMS, 1964; RYLE, 1970a; RYLE & POWELL, 1972). In S24 ryegrass, fully expanded leaves exported about 40% of their assimilate to tillers in their own axils or in the axil of the leaf below (RYLE & POWELL, 1974). The percentage of total shoot current assimilate moving down into the roots increases in vegetative tillers as the tillers become established. ROBSON (1973b) measured a translocation of only 5% to the roots in seedlings of perennial ryegrass whereas MARSHALL & SAGAR (1968a) found 25% in the youngest tillers increasing to 60% in the main tillers (*L. multiflorum*). The apparent 'priority' of shoot growth over root growth in the allocation of restricted amounts of assimilate is also suggested by the reduced translocation of ^{14}C to roots in lower light conditions (RYLE, 1970b).

Evidence for the movement of ^{14}C labelled assimilates from one tiller to another is somewhat conflicting. MARSHALL & SAGAR (1965) and WILLIAMS (1964) using the autoradiograph technique, and BARNABAS & STEINKE (1975) suggest there is no movement from one tiller to another once they are established. On the other hand, MARSHALL & SAGAR (1968a) using a quantitative ^{14}C technique measured considerable exchange between main and daughter tillers. The exchange resulted in net receipt by the main tiller (with its possibly larger sink of tiller buds) and, conversely, no net dependence of the youngest daughter tiller on the main tiller. RYLE (1972) and RYLE & POWELL (1974) also report considerable translocation (30% of current assimilate) to developing and rooted tillers, and CLIFFORD, MARSHALL & SAGAR (1973) found the movement to be two-way in young plants.

Roots of grasses, in contrast to those of legumes (e.g. HODGKINSON, 1969), do not re-export assimilates to shoot tissue. They are stated to be the main receivers of assimilates in young grass plants (MARSHALL & SAGAR, 1968a) and to be held in common between tillers of the same plant (TROUGHTON, 1960). The auto-radiographs of WILLIAMS (1964) show the imported assimilates to be highly localised at the growing root tips.

The distribution of assimilates in several grass species follows the pattern described above although absolute values vary (*Phleum pratense*: WILLIAMS, 1964; *L. multiflorum*: MARSHALL & SAGAR, 1968a; *L. temulentum*: RYLE, 1972; *L. perenne*: RYLE & POWELL, 1974; uniculm barley: RYLE *et al.*, 1973).

In Appendix 2 a table has been drawn up showing the relationship of different parts of the grass plant to the movement of assimilates and minerals, using S24 perennial ryegrass as the example. The continual cycle of leaves on a tiller, in which the production of new leaves is generally associated in time with the death of old ones, has been shown to be based on a genetically controlled sequence of enzyme production and physiological activity (see p.16). The activity of a leaf is thus closely identifiable with its position on the tiller. The relative activities, import and export of carbon compounds and order of priority over reserves when stressed, are given in this table for the different parts of the grass plant. The figures are taken from RYLE (1970a and 1970b); and from RYLE & POWELL (1974). The order of priority over assimilates is given by BEGG & WRIGHT (1964).

The main features to note from this table are

(i) the emerging and youngest fully expanded leaves provide 58 + 25 = 83% of the assimilate used in the terminal meristem. Removal of perhaps the 1st leaf, and particularly the first two leaves, could be expected to have a pronounced effect on weight per new leaf produced;

(ii) the emerging leaf is little involved in the supply of assimilate to axillary tillers whereas the two older leaves contribute considerably (about 36% each) to the import by the daughter tillers. We have seen, however, that due to the existence of a two-way flow between main and daughter tillers, it is unclear how dependent the daughter tillers are on assimilates from the parent tiller for growth (see page 74).

The distribution of assimilates is finely controlled as was clearly demonstrated by DOODSON *et al*. (1964); the mechanism of control has, however, still to be fully understood. Since the direction of assimilate distribution in grasses is not limited by vascular connections, the differential movement must be due to physiological causes (WILLIAMS, 1964). NEALES & INCOLL (1968) have reviewed the evidence for the hypothesis that the observed movement can be described in terms of 'sources' and 'sinks' - where sources are regions of higher availability and sinks are regions of higher demand for a particular transportable material. The youngest leaves tend to be the sources, being the most photosynthetically active (WOLEDGE, 1973; ROBSON, 1973b), but in completely defoliated plants storage organs become the major

sources e.g. fructosan accumulations in sheaths of temperate grasses. The order of priority, or of demand, over the receipt of assimilates is (1) the apical meristem and developing leaves, (2) increase in shoot dry weight (i) by leaves (ii) by stem internodes, (3) roots, according to BEGG & WRIGHT (1964).

The carbon economy of plant tissues appears to be further integrated in that the movement of assimilates from source to sink is thought to act as a feed-back on the rate of photosynthesis - though the evidence is circumstantial rather than proven (NEALES & INCOLL, 1968). It is suggested that a high concentration of assimilates in a photosynthetic organ inhibits the rate of photosynthesis, preventing any further accumulation of photosynthate (SWEET & WAREING, 1966). In water-stressed plants less translocation takes place (SOSOBEE & WIEBE, 1971) and net photosynthesis declines to zero below a certain water deficit (LUDLOW & NG, 1974). On the other hand, a large demand for assimilates continually removing the products of photosynthesis from the source can stimulate or maintain photosynthetic rates (inflorescence development: ONG & MARSHALL, 1975; defoliation: GIFFORD & MARSHALL, 1973; HODGKINSON, 1974).

3.3.3.2 THE EFFECT OF DEFOLIATION ON THE CARBON ECONOMY

The major physiological response of the plant to defoliation is an immediate temporary shift in the translocation of current and stored assimilates (RYLE & POWELL, 1975) in such a way as tends to maintain the relative growth rate of shoot tissue (TROUGHTON, 1957; A. DAVIES, 1974). The plant, rather than the individual tiller, becomes the integrated unit of growth (MARSHALL & SAGAR, 1965). Another important physiological response may be a

modification in the rates of photosynthesis although evidence on this is conflicting (RYLE & POWELL, 1975).

Growth of new shoot tissue takes place in the 'dark' within the tube of sheaths; it therefore requires a supply of simple sugars as an organic source of energy. The energy demands of meristematic and elongating cells appear to be met firstly from current and stored assimilates in any leaf tissue remaining, secondly from easily mobilisable materials accumulated in the base of the tiller, and thirdly, possibly, from the breakdown of proteins and structural material which may result in tiller death.

(a) Energy supply from leaf tissue remaining

Under partial defoliation, temporarily increased rates of export have been widely observed from the remaining leaves (SOSOBEE & WIEBE, 1971; RYLE & POWELL, 1975) and from adjacent tillers on the same plant (MARSHALL & SAGAR, 1968b; ROGAN & SMITH, 1974) particularly from the older leaves (GIFFORD & MARSHALL, 1973). Increased or maintained rates of photosynthesis supporting this increased export have been reported in maize, dwarf bean and willow by WAREING, KHALIFA & TREHARNE (1968); in lucerne - particularly in the younger leaves - by HODGKINSON (1974); and in adjacent tillers of *L. multiflorum* by GIFFORD & MARSHALL (1973). A. DAVIES (1974) suggests that the very small effect of partial defoliation on relative growth rates in S24 ryegrass could be explained in terms of increased activity in the remaining tissues. RYLE & POWELL (1975), however, always measured a drop of 5 - 10% in photosynthetic rate.

The importance of the amount of leaf tissue remaining after defoliation was stressed by BROUGHAM (1956). The hypothesis was

that maximum production is achieved when 95 - 100% of incident light is intercepted. Although gross photosynthesis increases with increasing Leaf Area Index up to 100% light interception (McCREE & TROUGHTON, 1966b; ROBSON, 1973a and 1973b), this does not itself lead to the conclusion that crop growth rates would be improved by leaving behind a certain amount of leaf tissue after defoliation (in order to intercept a substantial proportion of the incident light from an early stage of regrowth). It has been pointed out that a number of other factors influencing regrowth have to be taken into account (WILSON & McGUIRE, 1961; McCREE & TROUGHTON, 1966b; MORRIS, 1967; DE LUCIA SILVA, 1974). The leaf area remaining is generally inefficient due to previous shading or advanced leaf age (BROWN, COOPER & BLASER, 1966) although there is a certain increase in photosynthetic efficiency of these leaves when exposed to light (WOLEDGE, 1971). Moreover, the leaf tissue that is left behind constitutes a net loss from harvested dry matter yield since it dies and disappears into the soil (L.A. HUNT, 1965; McCREE & TROUGHTON, 1966b; SIMONS, DAVIES & TROUGHTON, 1972).

New photosynthetic tissue is expanded within a few hours at a rate of 0.5 $cm^2 h^{-1}$ (RYLE & POWELL, 1975). If the order of magnitude of the observations by RYLE & POWELL (1972) and BEATY *et al.* (1974) are taken into consideration, then at summer temperatures the amount of newly expanded tissue will soon be enough to supply much of the requirements of terminal meristematic growth. Meristematic cells start off with a very high concentration of water soluble carbohydrates anyway, at about 15 - 32% (DAVIDSON & MILTHORPE, 1966a). RYLE & POWELL (1975) found that

current assimilate in partially defoliated plants was sufficient to account for all observed growth, with no mobilisation, and new growth was 70 - 100% of that of intact plants. In winter it is perhaps unlikely that growth of new photosynthetic tissue would be fast enough and it may be expected that reserves will be drawn on sooner.

A plant with a larger leaf area remaining after defoliation may have a competitive advantage for light. However, in evaluating the importance of leaf area with respect to subsequent dry matter production or harvestable yield, senescence and death rates of old leaf tissue must be taken into account (MORRIS, 1967; DE LUCIA SILVA, 1974).

(b) Energy supply from accumulated materials (reserves)

So far, reference has largely been made to ^{14}C studies only. Contributions to the analysis of regrowth have also come from studies of stubble weight changes and water-soluble carbohydrate (WSC) content.

It appears that following defoliation accumulations of soluble carbohydrates are mobilized; the WSC content of stubble and roots falls for the first 2 - 4 days (A. DAVIES, 1965; ALBERDA, 1966; DAVIDSON & MILTHORPE, 1966a; WILSON & ROBSON, 1970). Some of this is used for stubble and root maintenance respiration, the demand in the roots apparently having to be met sometimes from substances in addition to WSCs (DAVIDSON & MILTHORPE, 1966b). With respiration using accumulates at the rates reported in legumes (HODGKINSON, 1969; PEARCE, FISSEL & CARLSON, 1969) it is reasonable to expect a fall in net content of WSCs at a time when the photosynthetic supply is low.

It seems likely that some of the water-soluble carbohydrates are also used for the initial regrowth following defoliation. Thus when defoliation is severe - all leaf laminae removed - leaf expansion is slower when the WSC content is low than when it is high (DAVIDSON & MILTHORPE, 1966a).

(c) Energy supply from structural material and protein

If no photosynthetic area is left after defoliation, including green sheaths, then the initial energy for expansion of new tissue must come from organic compounds. In defoliated plants the delay in onset of exponential growth (ALBERDA, 1966) is 7 days in plants of low WSC content compared with 4 days in plants of high WSC content. Accumulates must be broken down into simpler units before they can be transported; for this enzymes are necessary. It is interesting, though speculative, to note that PEARCE *et al.* (1969) measured a rapid rise and fall in the first three days after defoliation in a certain ^{14}C labelled fraction that may have been due to protein synthesis. The turnover was only observed in a second defoliation where stress on carbon reserves may have been greater. It remains a matter of speculation as to whether the initial delay in regrowth is due to an initial shortage of catabolic enzymes; and whether, in plants of inadequate WSC content, the synthesis of new enzymes capable of mobilising structural and protein material may cause an increased delay before energy is available to support growth of photosynthetic tissue. The suggestion seems far-fetched in view of the very rapid rates of biochemical changes relative to seven whole days; but there is a definite lag immediately followed by a growth rate similar to that in intact plants.

If water-soluble carbohydrate content is inadequate (less than 6 - 15%) there is indirect evidence that structural materials are mobilised, leading to 10% death of tillers within 2 days of defoliation, compared to only 23% 12 days later (ALBERDA, 1966). The products of protein breakdown can also be used for respiration (STEWARD, BIDWELL & YEMAN, 1958).

3.3.3.3 EFFECT OF DEFOLIATION ON THE REDISTRIBUTION OF MINERAL NUTRIENTS

When mineral nutrient supply in the soil is low, removal of the oldest living and senescent leaves has been found to reduce the weight of new leaves produced (DAVIDSON & MILTHORPE, 1966a: *Dactylis glomerata*; HOPKINSON, 1966: *Cucumis sativa*). In such circumstances the older leaves appear to play a part in regrowth by providing the more mobile mineral elements. However, in intensively grazed or fertilized pasture - as opposed to range grassland - this conservation of minerals within the plant is unlikely to be important.

3.3.3.4 THE EFFECT OF MORPHOLOGY ON REGROWTH

The regrowth response to a particular defoliation is also related to the plant's structure. A. DAVIES (1966) drew the tentative conclusion that the number of growing points appeared to be critical in determining the weight of regrowth. Since the development of some of the growing points, the tiller buds, is stimulated by greater light intensities at the base of the sward, WILSON & McGUIRE (1961) suggest that closer defoliation (i.e. removal of the leaf canopy) has, to some extent, a beneficial effect on regrowth in allowing greater light penetration.

The position of the shoot apex is crucial with respect to defoliation (I. DAVIES, 1972). In vegetative tillers the apex is normally below cutting or grazing height. In reproductive swards, however, the time and depth of defoliation in relation to stem extension has important consequences for production and persistency of the sward.

3.3.3.5 SUMMARY OF THE CONSEQUENCES OF DEFOLIATION BY CUTTING OR POSSIBLY UNDER INTENSIVE ROTATIONAL GRAZING

The consequences of defoliation that will be outlined here apply only to swards where all the tillers on a plant are defoliated within a day or two of one another. Under less widespread defoliation the increased translocation from, and perhaps photosynthesis in, uncut adjacent leaves and tillers may considerably modify the severity of the defoliation stress.

(a) Root growth

Root growth is the first growth parameter likely to be reduced in competition for fewer assimilates (CRIDER, 1955; ANSLOW, 1968; RYLE & POWELL, 1975). CRIDER found that it was not until more than 40% of shoot tissue had been removed that there was any reduction in root growth, but this is likely to vary with variety and species. Root growth stopped within 24 hours of a severe clipping (almost all leaves removed) and did not start again for 6 - 18 days (see also DAVIDSON & MILTHORPE, 1966b). The effect of reduced root growth must be to make the plant more susceptible, or less competitive, in times of water or nutrient shortage.

(b) Tillering

The effects of defoliation upon tillering are several, making analysis of any particular treatment difficult. On the one hand the increased penetration of light (WILSON & McGUIRE, 1961) and,

in a reproductive sward, release of some tiller buds from apical dominance (PHILLIPS, 1975), might be expected to increase tillering. On the other hand, increasing severity of defoliation may reduce the number of tillering sites through its effect on leaf appearance, and may reduce site utilization, possibly through a reduction in nutrient and energy supply (A. DAVIES, 1974).

Whatever the mechanisms controlling it, the rate of production of new tillers was one of the most sensitive factors affecting the weight of regrowth under different defoliation treatments (A. DAVIES, 1965, 1966, 1974).

(c) Leaf weight

Weight per new leaf does not appear to be affected until defoliation is severe (BEGG & WRIGHT, 1964; ANSLOW, 1968; SIMONS *et al.*, 1972), when weight is reduced. This appears to be particularly so when soil nutrient status is low (DAVIDSON & MILTHORPE, 1966a).

(d) Leaf appearance

There are conflicting reports on the effect of defoliation on the subsequent rate of leaf appearance. Since defoliation treatments and experimental circumstances differ, it is likely that a number of factors which govern the rate of leaf appearance are affected (ANSLOW, 1966), giving rise to individualistic results.

It could be expected, as BEGG & WRIGHT (1964), MORRIS (1967) and SIMONS *et al.* (1972) found, that leaf appearance would be the last growth parameter to be reduced by internal competition for energy and nutrients. In some cases, where defoliation has been severe, leaf appearance rate was reduced (DAVIDSON & MILTHORPE, 1966a; A. DAVIES, 1974) although SIMONS *et al.* found no effect and BEAN (1964) got an increased rate after a severe cut.

It may be that reduced ~~growth~~ appearance rates are attributable to inadequate WSC content. Increased rates may be caused by an increased temperature at apex level when shading leaves have been removed (PEACOCK, 1975b), or by a shorter tube of sheaths through which to grow (A. DAVIES, pers. comm.).

3.3.3.6 DEFOLIATION IN SWARD MANAGEMENT

One of the main aims in grassland management is to maintain a sward of high nutritional quality while at the same time aiming for as high yields as possible, given that condition.

It has been observed that animals tend to remove the younger, more digestible tissue. The heavier the grazing pressure, the more herbage will be removed and the lower will be the average quality of the plant remaining immediately afterwards. The quality and quantity of herbage available at a subsequent grazing will depend upon

(1) the amount of material left behind at the first grazing, and

(2) the time interval and regrowth between successive defoliations.

Severity of defoliation may affect the subsequent accumulation of leaf in two ways. On the one hand, the more shoot material left behind, the more senescent tissue there will be at a subsequent grazing (HODGSON, 1966). On the other hand, sufficient stubble must be left to support tiller survival and regrowth.

The weight of new growth produced is a function of

(i) number of tillers per unit area

(ii) weight per new leaf

(iii) number of new leaves produced per tiller.

(i) The number of tillers per unit area is made up of:

old tillers surviving after defoliation, i.e. those with apex below cutting height (see Section 3.3.3.4), and sufficient photosynthetic capacity or mobilisable reserves to support terminal meristematic activity until some new leaf has emerged (see Section 3.3.3.2).	+	new tillers developing after defoliation (see Section 3.3.3.5(b)). Tiller development is a function of available tillering sites, release from any apical dominance, and nutrient supply to support their growth.

(ii) The weight of new leaf produced is partly dependent on the severity of the defoliation stress (see Section 3.3.3.5(c)) and partly dependent on current conditions for photosynthesis.

When a tiller is defoliated, the severity of the stress depends on the avilability of substrate energy from the rest of the plant to support continued meristematic growth (see Section 3.3.3.2). The main difference between grazing under rotational conditions and grazing under set-stocking is the severity of defoliation experienced by a plant within one day (see MORRIS, 1967, set-stocking; compared with DE LUCIA SILVA, 1974, strip grazing). Under set-stocking, as compared to rotational grazing, it is more likely that a tiller will only be partially defoliated on any one occasion, and that some of the adjacent tillers on the same plant will remain intact. Regrowth is likely to be supported by an immediate supply of

assimilates from adjacent leaves and intact tillers (MARSHALL & SAGAR, 1968b; RYLE & POWELL, 1975). Relative growth rate may be more speedily restored (ALBERDA, 1966) to equal that of intact tillers, and sward persistency may be favoured. If herbage is grazed in patches, however, as in the set-stocked swards of MORRIS (1967), then the situation is not so clear. Defoliation stress within a patch may be severe since there will be fewer tillers, and perhaps leaves, left ungrazed. SMITH (1972) found no difference in overall yield between patchily and uniformly cut swards although SMITH & MACAULEY (1975) did observe some interaction in regrowth between adjacent areas defoliated to different extents.

(iii) The number of leaves produced per tiller is governed by the length of the time interval between successive defoliations relative to the rate of leaf appearance (see Section 3.3.3.5(d)).

It has been suggested that a defoliation interval corresponding to the growth of three new leaves would be appropriate in a vegetative sward (A. DAVIES, 1971a). In this way the increase in shoot weight due to successively larger leaves, and to the establishment of new tillers, would be accumulated until weight loss from senescence began to be counterproductive. In other words, it is suggested that maximum utilization of herbage production would be achieved if the herbage is harvested as soon as the ceiling yield is reached; if harvested earlier, the potentially greater weight of the third leaf would not be attained; if harvested later, other material would be lost by senescence. In one experiment this three-leaf concept appeared to hold but further experiments by DAVIES (personal communication)

have failed to support it. Logically it would appear that the continuing increase in ceiling yield once the balance number of leaves is attained must be due to continuing increases in tiller numbers and tiller size (particularly of the new daughter tillers).

In grazing practice, a defoliation system based on harvesting the herbage as soon as the ceiling yield is reached requires rotational, once-off grazing. In such a system, the intake of the animal is often limited as a consequence of ensuring that most of the accumulated, highly digestible, standing crop is removed. Apart from considerations of sward regrowth this may reduce production per animal because of reduced intake, though production per hectare may increase. More frequent, less severe, defoliations per tiller may be imposed by a continuous grazing system. In such circumstances herbage production may be lower but, at low grazing pressures, animal intake would be less limited.

In practice, animal performance under intensive grazing management appears to be similar under rotational and strip grazing systems versus set-stocking (WHEELER, 1962 : review), or up to 10% greater (HOLMES, 1962 : dairy cattle). However, as HOLMES points out, the increased management costs of rotational grazing may offset production increases depending on economic circumstances.

In less intensive systems, or under extensive grazing where pasture utilization cannot be closely matched with plant growth over short periods of time, there is a build-up of dead stem and leaf. The quality of the animal's intake

is reduced (EADIE, 1967) and the development of new tillers may be inhibited (WILSON & McGUIRE, 1961). One of the techniques used in the improvement of indigenous hill pastures is the severe grazing down of the pasture mat by animals with a less critical nutritional demand in relation to their maintenance and production requirements, e.g. store cattle (EADIE & BLACK, 1968).

CONCLUSIONS FROM LITERATURE REVIEW

A model of grazed pasture should be based on the tiller as the unit of production, since it tends to develop as a unit of independent integrated growth. Under partial defoliation, however, it is also necessary to relate the tiller to the plant as the integrated unit.

The unit used to model grazing, on the other hand, should be the leaf (and stem if present). It is at this level that selection, and the regrowth response of the plant, operate.

In preliminary modelling of sheep production from grazed pasture (in which intake was related to digestibility of ingested material), information upon the digestibility and rates of change in digestibility of leaves at different positions on the tiller was found to be crucial, but lacking. Furthermore, both MORRIS (1967) and DE LUCIA SILVA (1974) stress the importance of including loss of material by senescence and death when considering pasture production and its availability at any point in time to the animal. They both conclude that it has been given too little attention.

The experiments described in this thesis examine the passage of dry matter through a sward from its appearance as young leaf to its disappearance into the litter layer. Quantitative analyses are carried out into the 'availability' or distribution of digestible dry matter within the sward, and into the rates with which it is changing. Variations throughout the year, with nitrogen fertilizer applications, and with the development of reproductive tillers, were examined in Experiment 1. In Experiment 2 the effects of partial defoliation on sward structure, in terms of dry matter weight and quality, were examined.

CHAPTER FOUR

EXPERIMENT 1

An investigation into the sward structure and digestibility changes within an S24 perennial ryegrass sward throughout the year under four levels of nitrogen fertilization.

4.1 INTRODUCTION

Consideration of the requirements to be met by a model of the pasture component in a grazing system led to the conclusion that the sward should be represented at the detailed morphological level of leaf and tiller.

The literature was studied for information and understanding that would enable the construction of such a model. It was found that there was insufficient information available on the distribution of digestible dry matter within the sward and on how the distribution is affected by seasonal changes and management practices.

Accordingly, an investigation was set up to gain quantitative measures of the digestibilities and weights of plant parts as they aged and passed through different positions in the sward.

S24 perennial ryegrass was chosen as the variety for investigation. It is widely used in pastures, having the recommendations of perennial growth with high productivity and digestibility. S24 begins net dry matter production early in the year, shows good regrowth after cutting, and is palatable. It is used in both lowlands and uplands but has the drawback in the uplands of being somewhat susceptible to winter kill.

A second, important, consideration behind the choice of S24 as the experimental material is the large amount of agronomic and physiological work that has already been done on the variety. This work can be referred to in developing the model.

4.2 MATERIALS AND METHODS

The investigation was carried out on a temporary ley of S24 Aberystwyth perennial ryegrass, located at Bush Estate, Penicuik, Midlothian. The site was an exposed lowland field 200 m above sea-level, sloping very gently down from west to east. The soil was a dark grey/brown sandy loam of the Macmerry series, derived from carboniferous sediments and generally imperfectly drained. Surface water did not accumulate on the experimental site.

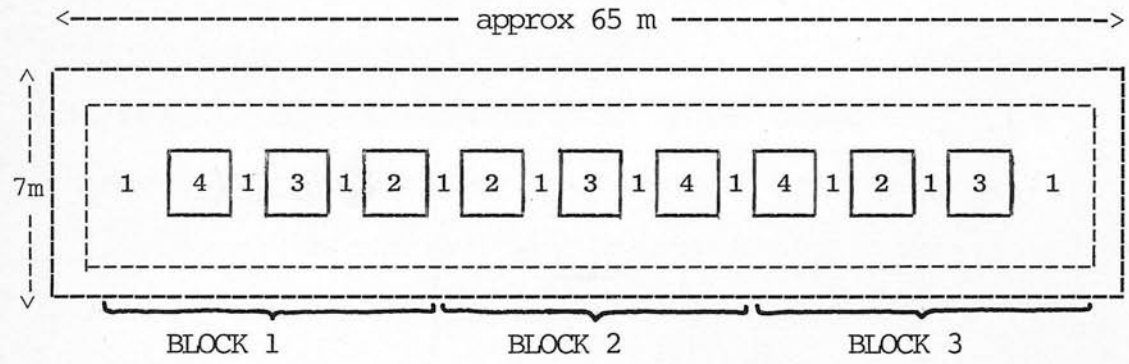
Wheat had been grown the previous year, 1973, and had been undersown with S24 Aberystwyth perennial ryegrass. At the end of February 1974 tillering was still patchy with bare areas and a small amount of *Poa annua* interspersed.

Preliminary observations were made at the end of February. On 1st April 1974 the field was rolled and dressed with 250 kg ha^{-1} of Fisons Extra Grass 29-5-5 prior to setting out the experimental area.

Fig. 4.2.2 : Block 3 in June 1975. The far plot was left uncut in 1975. The middle plot is treatment N2, the nearest N4, and the gaps in between are N1.

4.2.1. LAYOUT OF EXPERIMENT

Three blocks of three plots were laid out in a strip along the contour of the field and away from the hedges. In this way all plots were subject to similar drainage and exposure. A fence was erected on June 28th 1974 to keep out rabbits and sheep. The layout is shown in Fig. 4.2.1.



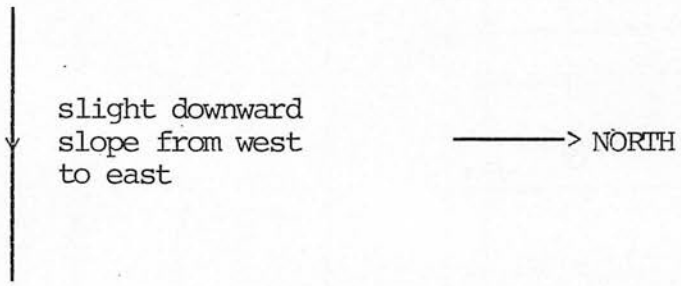


Fig. 4.2.1: Layout of experiment, showing plots (1, 2, 3, 4 = nitrogen treatments) and blocks.

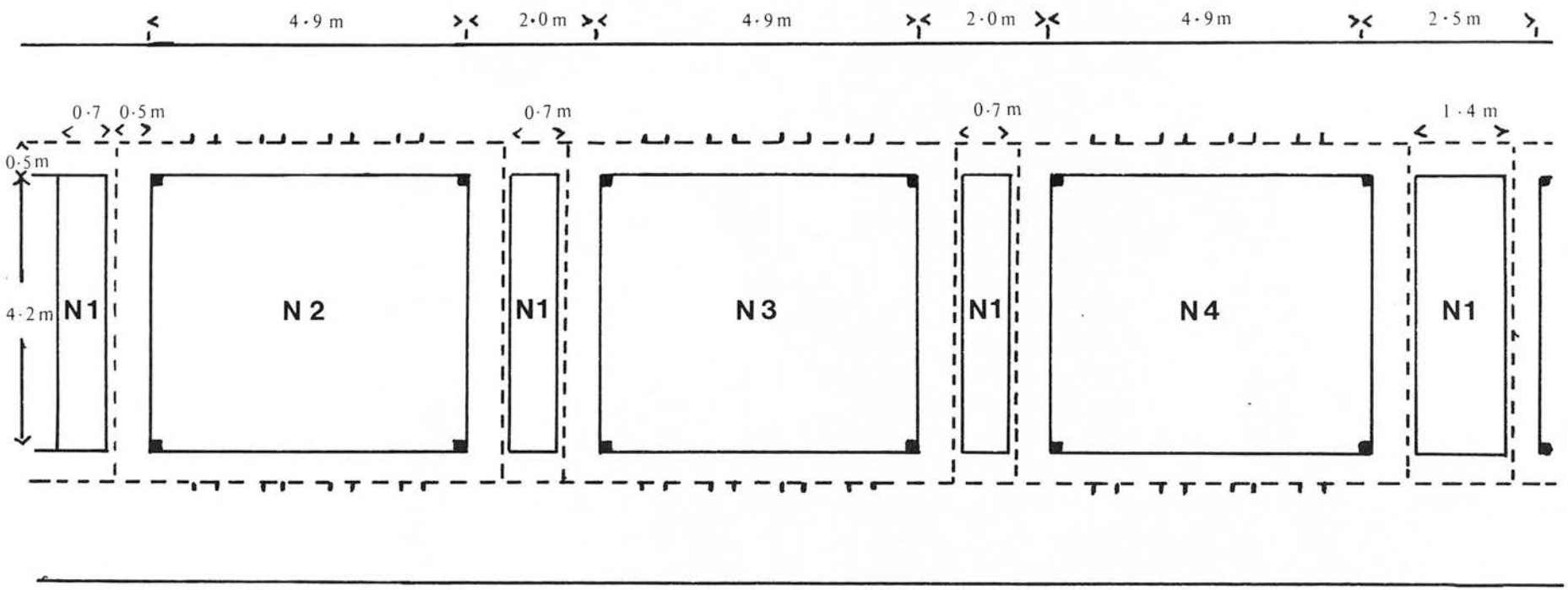


Fig. 4.2.3 : Layout of a block

■ Corner posts of treatment plots

Path markers

Area within which fertilizer treatment was applied,
i.e. 0.5 m border around edge of plot.

Each block contained three nitrogen treatment plots 4.20 m × 4.90 m with a gap of 2 m between each of them. Three nitrogen treatments were allocated at random to the plots within a block. Each block was separated by a gap of 2.5 to 3.0 m.

Nitrogen fertilizer treatments were applied at the beginning of May 1974 after the whole experimental area had been cut to 4 cm. The fertilizer was spread on an area extending 0.5 m beyond the sides of each plot. A gap of 1 m was left cut but unfertilized between each plot.

Soon after the fertilizer treatments were first applied, the range of fertilizer levels examined was extended by incorporating a low-nitrogen treatment into the experiment. By splitting this treatment plot up into columns it was possible to fit it into the unfertilized gaps between the other treatments (see Fig. 4.2.3).

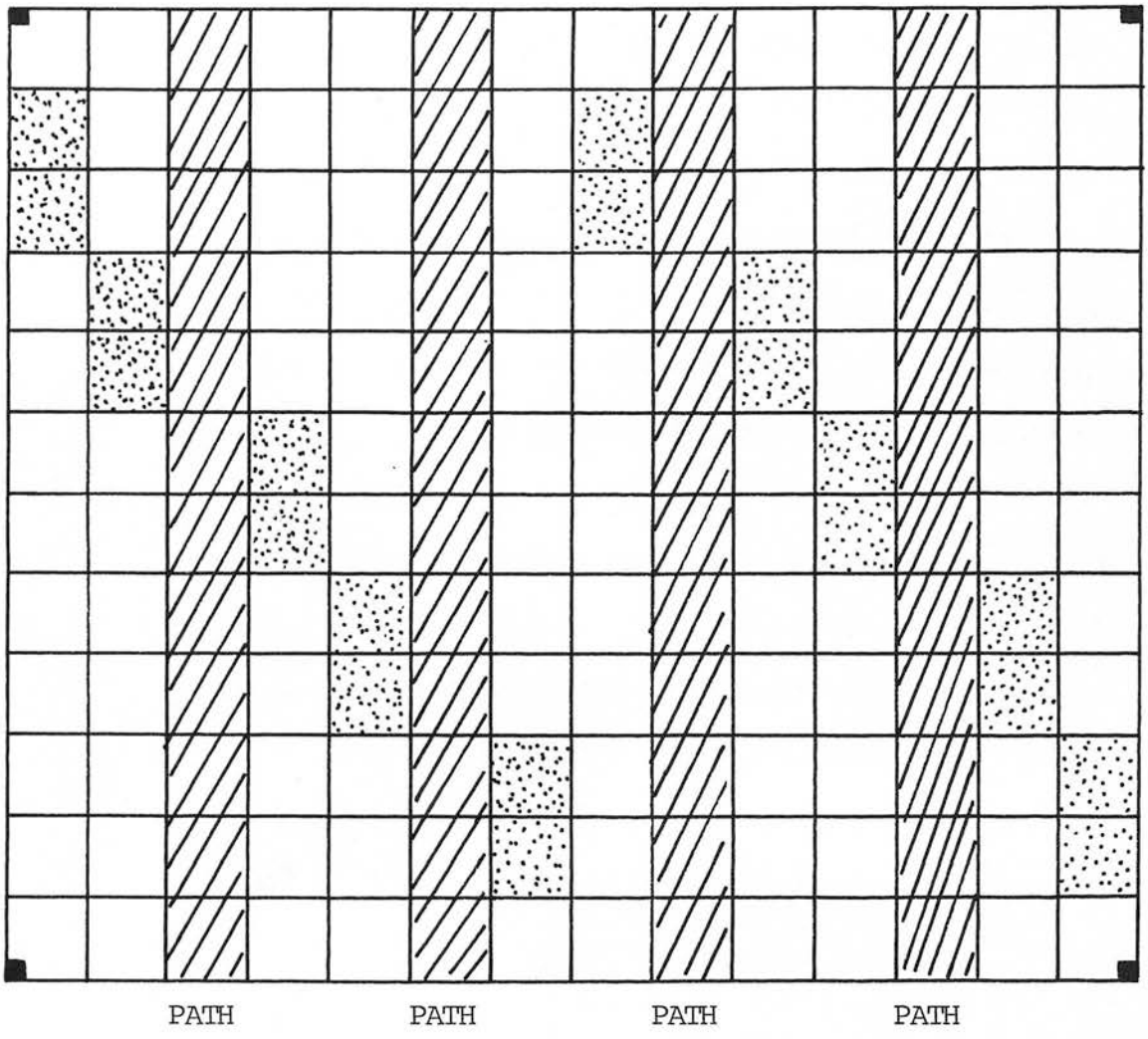


Fig. 4.2.4 : Layout of a treatment plot.

One plot contains 120 subplots of size 0.35 × 0.35 m.

20 of these, as shown by , contain the permanently ringed tillers.

■ Stakes marking plots.

--|--|- Stakes marking paths.

Each treatment plot was divided up conceptually into 120 subplots 0.35 m × 0.35 m in size (Fig. 4.2.4). 100 subplots were for yield sampling. The other 20 were devoted to tiller sampling, including observations on permanently marked tillers for leaf appearance, and small-scale harvesting for sward structure and digestibility analysis.

The shape and size of the subplots were determined by yield-sampling considerations. Square subplots at least 0.35 m wide could be cut equally from two directions. Prostrate tillers would then be picked up irrespective of the direction in which they faced.

The number of yield subplots allowed for ten cutting dates with 10 samples being taken on each date. A preliminary trial had shown that at least 10 samples were needed to give a reliable estimate of the mean yield.

The number of tiller-sampling subplots was governed by the consideration that no more than 5% of the tillers in it should be removed on any one occasion. Adopting a subplot size of 0.35 m × 0.35 m, and on the conservative estimate of 5,000 tillers m^{-2}, a sample of 600 tillers for digestibility analysis could be removed from a total of 21 subplots without disturbing the cover of the sward.

600 tillers = 5% × 5000 tillers m^{-2} × total sampling area

$\therefore$ total sampling area required = 2.4 m^2

and 2.4 m^2 = (0.35 × 0.35) × 19.59 subplots.

The subplots were arranged in 10 columns and 12 rows. Two subplots in each column were reserved for tiller sampling. These areas were distributed regularly across the plot to cover any east-west and north-south gradients.

The remaining subplots were allocated to yield sampling dates. Each date was represented by one subplot in every column. Within a column, dates were allocated to rows at random. (See section 4.2.3.3, p.106).

Four paths were inserted between columns to minimise variation due to treading.

4.2.2 SWARD MANAGEMENT : CUTTING DATES AND FERTILIZER TREATMENTS

The management of the sward was aimed at maintaining a largely vegetative tiller population. From May 1975, cutting and fertilizing of the third nitrogen treatment (N3) were discontinued, however, and these plots were used for gathering observations on reproductive tillers.

Grass cutting

The experiment ran from May 1974 till early July 1975 and the cutting dates were as follows :

4.5.74, 25.5.74, 28.6.74, 20.8.74, 7.11.74 and 15.5.75.

The decision to cut was made for one of three reasons :

(a) to prevent the development of reproductive tillers by removal of the apex when stem elongation began (May and August cuts);

(b) to prevent sward deterioration due to lodging and thinning of the tiller population (JACKSON, 1974) (June cut);

(c) to minimise winter kill (BEDDOWS & JONES, 1958) (November cut).

Only one cut was necessary in 1975 because the growing season was later and shorter.

A Mountfield rotary lawnmower was used in 1974 and a Brot (miniature forage harvester) in 1975. The plots were cut to 4 cm and cut material raked off.

Fertilizer applications

The whole area was fertilized at the beginning of the growing season each year (3.4.74 and 17.4.75) with 250 Kg ha^{-1} of Fisons Extra Grass 29-5-5 (73 Kg N ha^{-1}, 12.5 Kg P ha^{-1} and 12.5 Kg K ha^{-1}).

Subsequent to this, nitrogen fertilizer was applied in the form of Nitram at four levels twice a year after the grass had been cut :

	Treatment Kg N ha^{-1}			
Date of application	N(1)	N(2)	N(3)	N(4)
1974 1975				
3.4.74 and 17.4.75	73	73	73	73
6.5.74 and 16.5.75	0	67	135	202
23.8.74	22	45	67	90
Total per annum	95	185	275	365

Table 4.2.1: Nitrogen fertilizer applications, Kg N ha^{-1}

Each treatment area was divided up into quarters and the fertilizer spread by hand.

The soluble nitrogen content of the soil was determined at intervals throughout the year (See section 4.2.3.4, p.107).

Ringed tiller used for recording dates of appearance and death of successive leaves.

4.2.3 SAMPLING METHODS

Two types of sampling were carried out on the ryegrass :

(1) Continuous records were kept of the dates of leaf appearance, leaf death and tiller production, using sets of permanently labelled tillers (Section 4.2.3.1).

(2) At regular intervals of time the structure of the sward was examined in detail. Leaf heights and weights were measured and the digestibilities of the different parts were determined (Section 4.2.3.2). Yield to ground level was also measured each time sward structure was analysed (Section 4.2.3.3).

In the intervals between sward samplings, the soil was analysed for soluble nitrogen content (Section 4.2.3.4).

Meteorological information was available from the Meteorological Station on Bush Estate (Section 4.2.3.5).

4.2.3.1 RECORDS OF LEAF APPEARANCE, LEAF DEATH AND TILLER PRODUCTION

34 tillers per plot (102 per treatment) were monitored for dates of leaf appearance, leaf death, and tillering.

Fig. 4.2.4 shows the distribution of the 20 subplots containing labelled tillers. One or two tillers were located in each subplot using a random number grid. A coloured telephone-wire loop, followed by a ring made of red plastic tubing, was slipped over the tiller down to the base. The red plastic rings were numbered from 1 to 102 to identify the tiller. Red was used to help the observer find the tiller, but it also proved attractive

to birds who occasionally removed them. The telephone-wire ring was less easy to remove and therefore helped safeguard against the loss of a tiller record. In spite of this precaution, a number of observation sequences were terminated by ring removal.

The labelled tillers were located in the same positions in every plot so that the recorder could easily learn where to find them.

Tillers were examined once every two days during periods of rapid growth and about once every four days over the winter. When a new leaf was observed, the date of its appearance was recorded and a telephone-wire ring was hung on the leaf below; a note was made of its colour. When a leaf had turned completely brown the date of its 'death' was written down and the wire ring on it was removed.

A tally of tillering was also kept, the date being recorded when a daughter tiller was first observed.

Observation of a particular tiller was discontinued for one of the following reasons :

(i) Mechanical - ring lost when the grass was cut.

(ii) Animal - ring removed or tiller eaten by intruding rabbits, sheep or birds; tiller submerged by earth-worm activity; emerging leaves severed by wire-worm.

(iii) Plant - death of tiller from fungus, wilting, or other cause.

(iv) Tiller had become reproductive. In 1975, however, observations were maintained on reproductive tillers in the discontinued N3 plots. These plots were left uncut and unfertilized.

The date and reason for discontinuing observations on a tiller were noted down and records were begun on an adjacent vegetative tiller.

Field observations were transferred to record sheets indoors. An individual sheet was kept for each tiller :

AGE OF LEAVES

EXPERIMENT	TREATMENT	BLOCK	PLOT	TILLER
1	3	1	1	17

Position of tiller in sward : 90 Area 10

Date of appearance of daughter tiller	Leaf No.	Ring Colour	Date of leaf appearance Year	Day	Date of leaf death Year	Day	Supplementary Information
	1	red	1	131	1	181	131 - point
	2	blue	1	141	1	201	141 - 2 cm
1 145	3		1	153	1	206	153 - 1 cm
	4						
	5						

The supplementary details were helpful in interpreting field information where, for example, a ring had been lost or two new leaves had appeared.

The observations were coded on to computer punch cards. Programs were written to calculate, for every week of the experiment, the following information :

(i) leaf appearance interval, leaf death interval and leaf lifespan;

(ii) number of live leaves per tiller (where dead = 100% brown);

(iii) the mean ages of the last seven leaves to appear (where the mean age of the last leaf to appear = the mean age of the emerging leaf);

(iv) number of vegetative and number of reproductive tillers observed in that week.

Calculations were performed on vegetative or reproductive tillers as required.

4.2.3.2 SWARD STRUCTURE

Sampling dates are given in Appendix 3. From May to early October 1974 sampling took place every time a full complement of leaves had grown per tiller since the previous grass-cutting, i.e. after three new leaves had appeared and expanded. The sward was cut immediately after sampling between May and August. From October 1974 onwards, the plots were sampled more frequently - once a month, in order to follow changes throughout the year more closely. Inevitably this introduced cut leaves into some samples; their presence was recorded so that weights and heights would only be quoted for largely intact leaves.

Tillers were collected from subplots that had not yet been harvested to ground-level for yield estimation. Sampling positions were located at random. At each sampling position a clump of tillers 2 cm in diameter was cut off close to the ground. Clumps of tillers were collected until there was sufficient volume of

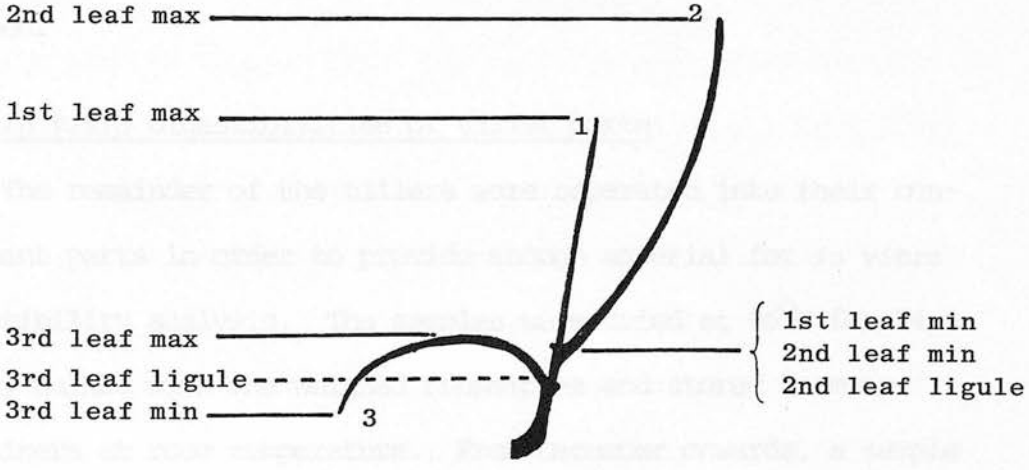
material on which to carry out *in vitro* digestibility analyses of the separated parts (about 30 to 40 g fresh weight).

Plot samples were put into polythene bags and kept in an insulated box containing frozen Freezela bags. On return to the laboratory the samples were transferred to a fridge at 4°C for up to 24 hours before being analysed.

Measurements

The tillers were mixed up in the bag and a subsample of 54 tillers was withdrawn. Reproductive tillers were kept separate from vegetative ones. The earliest criterion that could be used to distinguish reproductive tillers from vegetative ones was the presence of a white hard joint when the leaves were pulled away. If sufficient reproductive tillers were available, an analysis was done on them as well.

(a) Heights of leaves



The tillers were laid out against graph paper, as far as possible in the attitudes in which they grew in the field. The following heights were measured:

	1st leaf	2nd blade	3rd blade	4th blade
Maximum ht.	✓	✓	✓	✓
Minimum ht.	✓	✓	✓	✓
Ligule ht.		✓	✓	✓

(b) Weights of leaves

After measuring the leaf heights, the 54 tillers were separated into:

1st leaf
2nd blade
2nd sheath
3rd blade
3rd sheath
4th leaf
Dead older leaves + standing litter.

The separated parts were dried at 85°C for 24 hours, and weighed.

(c) *In Vitro* Digestibilities of tiller parts

The remainder of the tillers were separated into their constituent parts in order to provide enough material for *in vitro* digestibility analysis. The samples were dried at 85°C for 24 hours, bulked with the weighed subsamples and stored in mono-containers at room temperature. From December onwards, a sample of whole tillers was also dried for *in vitro* digestibility analysis.

Samples were dried at 85°C rather than 100°C since they were to be analysed for *in vitro* digestibility. VAN SOEST (1965) has shown that there are some changes in bound protein and apparent

lignin contents when wet (80% moisture) herbage is dried at higher temperatures and that such changes could affect digestibility. The precaution of drying at a cooler temperature was taken although TILLEY & TERRY (1968) found drying at 100°C had little effect on digestibility.

Preparatory to analysis, samples were milled in a Jansen and Kunkel water-cooled mill. The very small size of the samples (1 to 3g) necessitated the use of a mill which

(a) had a small chamber

(b) had little wastage.

A rubber bung was used to reduce the size of the milling chamber. Samples were ground until they had been reduced to a fine particle size. A trial run, in which milling time and particle size were varied, showed that neither had any effect on the digestibility of the ryegrass except when the sample was seen to be particularly poorly and unevenly ground.

The samples were analysed for *in vitro* dry matter and organic matter digestibilities according to the method of TILLEY & TERRY (1963) as modified by ALEXANDER & McGOWAN (1966). A set of standards of known *in vivo* digestibilities were analysed in each *in vitro* run. After each run a regression equation was calculated relating the observed *in vitro* digestibilities of the standards to their known *in vivo* digestibilities. The *in vitro* digestibilities of all samples were then corrected to standardised values using the regression equation for that particular run. An interactive computer program was written in FORTRAN to do all the calculations.

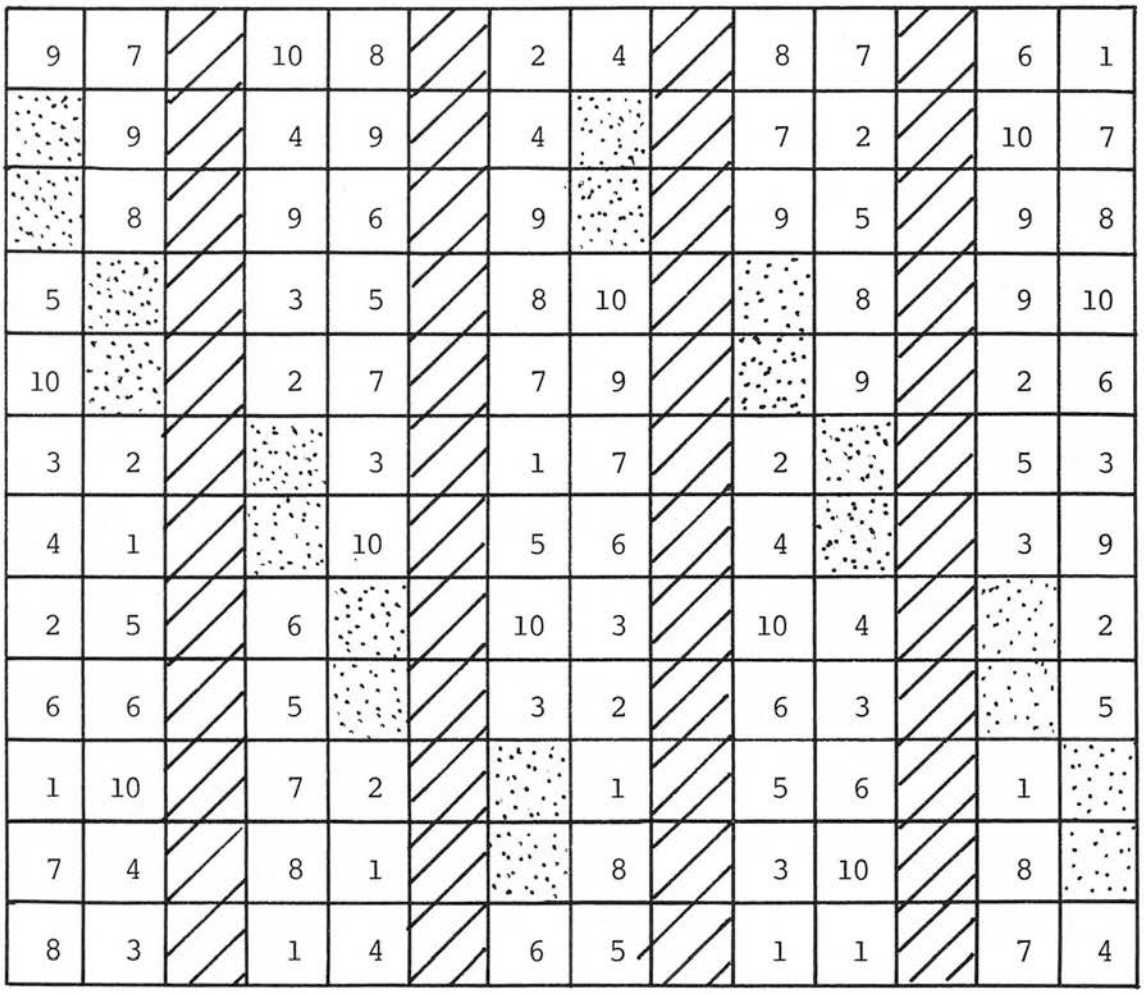


Fig. 4.2.5: Sampling positions for yield.

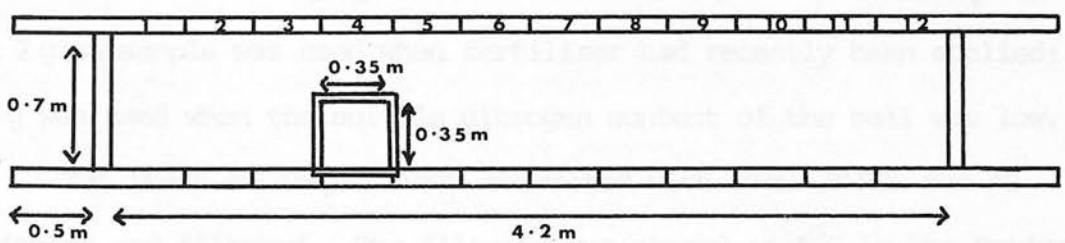
Every sampling occasion (1-10) is represented once in each column. Within that column the numbers are allocated at random.

4.2.3.3 YIELD

The dry matter yields of the plots were estimated every time an analysis was made of sward structure.

A master plan was drawn out at the beginning of the experiment showing which subplots were to be harvested on each of ten sampling occasions (See Fig. 4.2.5).

10 subplots per plot were cut to ground level using battery-powered Wilkinson Shears. A lightweight Dexion frame was used to locate the squares. The frame corresponded to two columns and twelve rows of subplots; it fitted between two paths, resting its ends on the path markers:

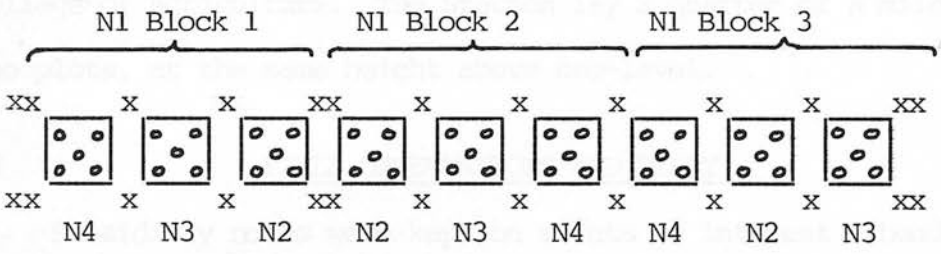


A quadrat 0.35 m × 0.35 m was fitted over the subplot to be cut.

Samples were dried at 100°C for 24 hours and weighed. Yield was expressed as Kg dry matter per hectare.

4.2.3.4 SOLUBLE NITROGEN CONTENT OF SOIL

The soluble nitrogen content of the soil was determined in each plot mid-way in time between sward-structure samplings.



x 8 cores taken from each replicate of N1

o 5 cores taken from each plot of the other treatments

Fig. 4.2.6: Layout of samples

Cores 10 cm deep × 3.5 cm diameter were taken and cut into 2 sections : 0-5 cm and 5-10 cm. Cores within a plot were bulked.

The samples were extracted the same day. The soil was pummelled and thoroughly mixed before weighing out two subsamples. A 2 g subsample was used when fertilizer had recently been applied; 4 g was used when the soluble nitrogen content of the soil was low.

The fresh subsamples were extracted with 20 ml 2N KCl for 40 minutes and filtered. The filtrate was stored at $4^{o}C$ in the fridge until it was analysed. A trial showed that delaying the analysis by six weeks did not affect the result. Usually, however, the analysis was carried out straight away.

Soluble nitrogen (NH_4^+ and NO_3^-) was determined by the micro steam distillation method as detailed by BREMNER (1965). Results were expressed as ppm soluble-nitrogen on an oven-dry ($100^{o}C$) soil basis.

4.2.3.5 METEOROLOGICAL RECORDS

Records from the Meteorological Station situated on Bush Estate were kindly made available by Mr. Affleck of the East of Scotland College of Agriculture. The Station lay a quarter of a mile from the plots, at the same height above sea-level.

4.2.3.6 FIELD OBSERVATIONS AND DIARY

Subsidiary notes were kept on events of interest - heading date, colour of sward, apparent surges in growth rate, weather phenomena, soil-cracking, earthworm activity, pests, etc.

A summary of sward management and sampling dates is given in Appendix 3.

4.2.4 STATISTICAL ANALYSES

Differences between nitrogen treatments were tested by Analysis of Variance when numbers of observations were sufficient ($n > 25$) to justify using the means from each plot as the values of the dependent variable. There were thus three blocks with four means in each block, one per treatment. The mean square between treatments was tested against the residual mean square. An Analysis of Variance program written by Miss S. Lutkins of the Statistics Department, University College of Wales, Aberystwyth, was used.

When observations per plot were fewer than 25 and there was a trend apparent across nitrogen treatments that was biologically related to the time of fertilizer application, then t-Tests were used to test differences between pairs of nitrogen treatments. The t-Test was carried out as described by BAILEY (1959) for small samples, in which the number of degrees of freedom is

calculated from the following formula :

$$d.f. = \frac{1}{\frac{u^2}{n_1 - 1} + \frac{(1-u)^2}{n_2 - 1}}$$

where $$u = \frac{s_1^2/n_1}{s_1^2/n_1 + s_2^2/n_2}$$

and s_1^2 = variance of sample 1

s_2^2 = " " " 2

n_1 = number of observations in sample 1

n_2 = " " " " " 2

The correlation between leaf appearance and leaf death intervals (see Section 4.3.2.5) was calculated using the routine provided by the STATISTICAL PACKAGE FOR SOCIAL SCIENCES, MARK 6.

4.3 RESULTS. EXPERIMENT 1.

4.3.1 METEOROLOGICAL CONDITIONS

4.3.1.1 Temperature (Figure 4.3.1)

The mean maximum daily temperature per week rose above 6°C throughout most of the year. From mid-May till the end of September 1974 maximum daily temperatures were approximately 16°C; they then fell quickly to an average of about 7°C through the winter up until Week 15, mid-April 1975. Maximum temperatures in May and early June 1975 (13°C) were similar to those in 1974 (14°C) but were 2°C warmer from mid-June to mid-July (18°C : 1975; 16°C : 1974).

The mean minimum daily temperature varied between 6° and 10°C from mid-May to late September 1974. From October 1974 till June 1975 it remained below 6°C, apart from a couple of weeks in late April.

Soil temperature at a depth of 5 cm followed the air maximum over the summer months, but was cooler by about 2°C; over the winter months it followed the air minimum plus about 1 - 2°C.

4.3.1.2 Sunshine hours (Figure 4.3.2)

From the beginning of October 1974 through to late February 1975, the hours of sunshine per week were low (2 - 20 hours). A small increase took place over March and April, but it was not until late April (1975) or mid-May (1974) that they rose to levels of 30 - 60 hours per week.

4.3.1.3 Daylength (Figure 4.3.2)

The number of hours between sunrise and sunset are plotted at weekly intervals in Figure 4.3.2.

4.3.1.4 Rainfall and accumulated soil moisture deficit

(Figure 4.3.3)

The soil moisture deficit was calculated for each week using tables given in M.A.F.F. (1967) Technical Bulletin No. 16, adjustment being made for actual sunshine hours. Weeks of moisture stress, i.e. weeks when growth is likely to have suffered because actual transpiration was less than potential transpiration, are indicated in Fig. 4.3.3 by the letter S.

Transpiration is reduced below the potential rate when the accumulated soil moisture deficit exceeds 50 mm - unless the amount of rain that falls in a 50+ deficit-week is greater than the potential transpiration expected during that week (e.g. week 25, 1974).

Periods of moisture stress occurred from the second week in May till the end of June 1974, from mid-July until the end of August 1974, and from the second week in June 1975 until after the end of the experiment. In weeks 26 and 35 1974, and 24, 26 and 27 1975, actual transpiration would have been reduced to almost half of the potential transpiration.

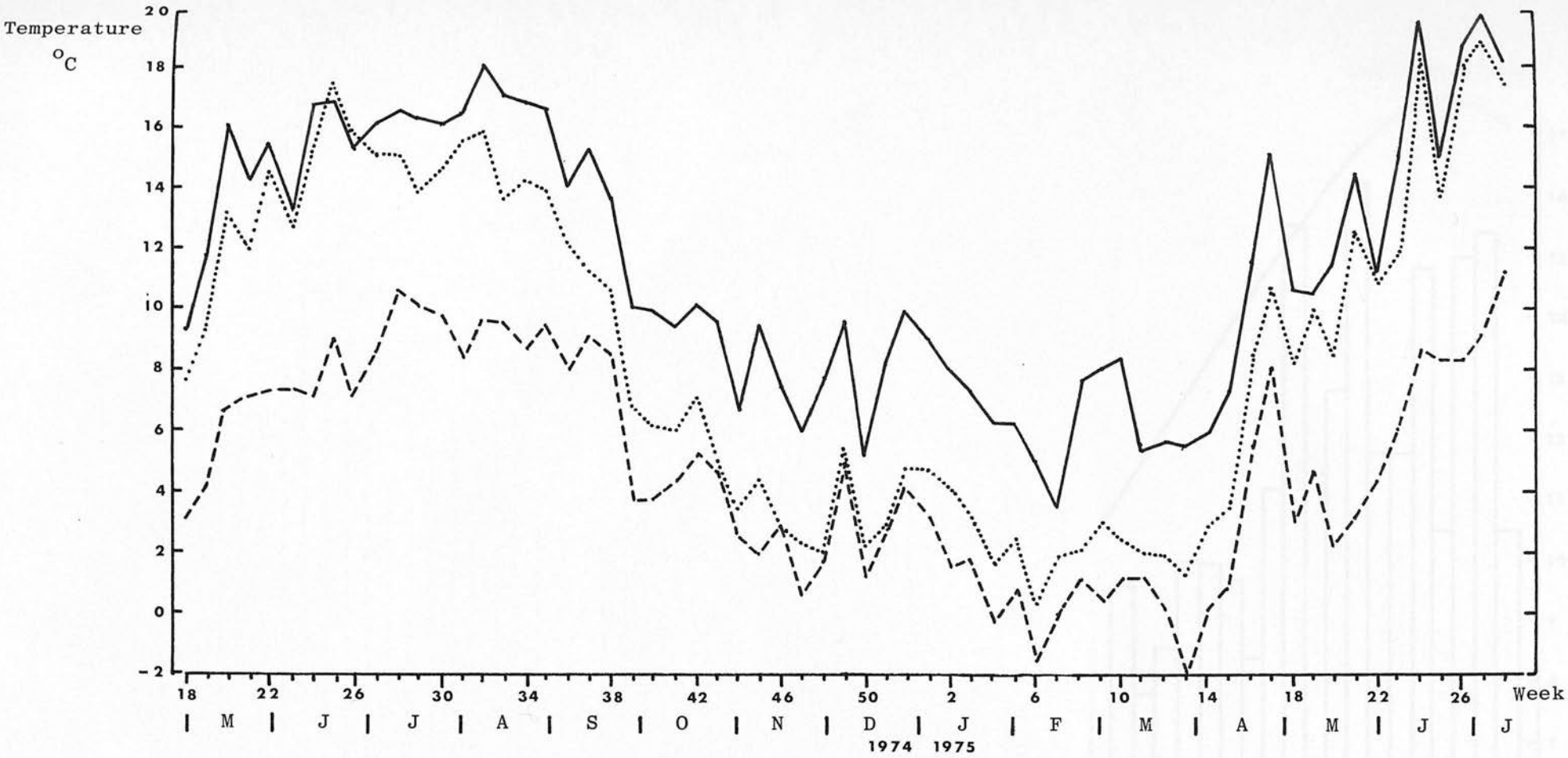


Fig. 4.3.1 : —— Maximum temperature ----- Minimum temperature

····· Soil temperature at 5 cm depth.

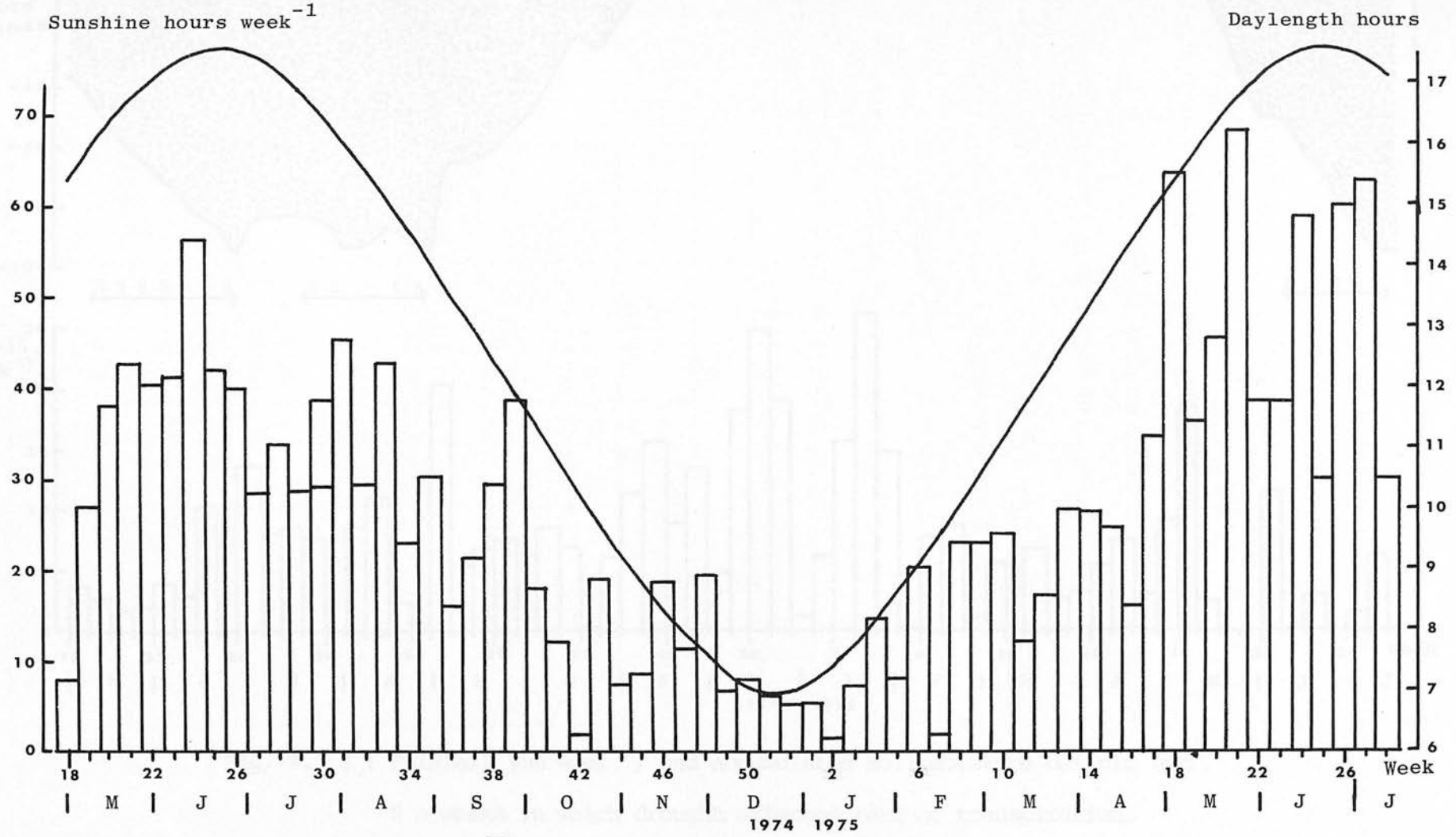


Fig. 4.3.2 : Sunshine hours per week.

Daylength - number of hours between sunrise and sunset (from WHITAKER'S ALMANACK, 1977).

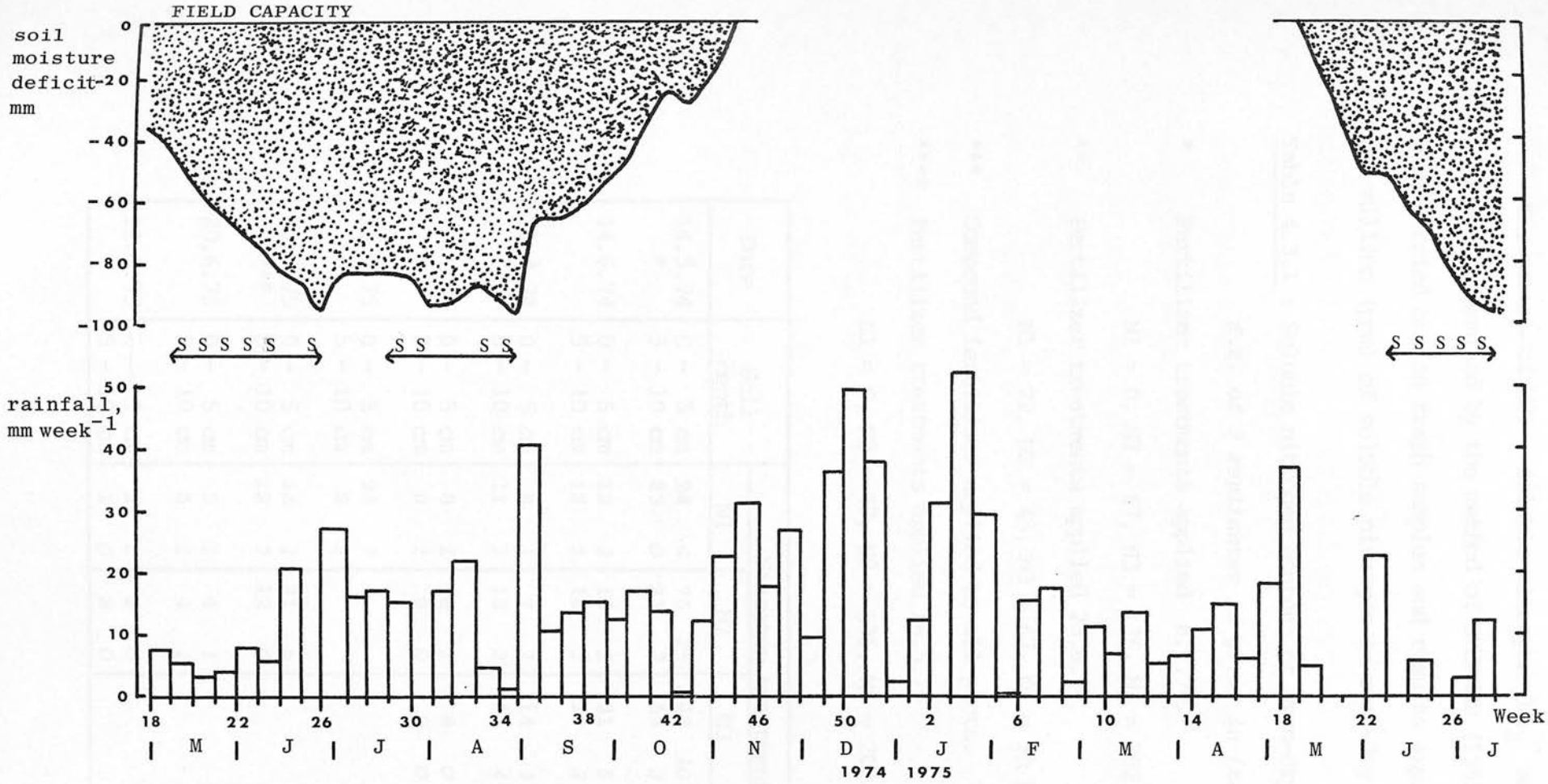


Fig. 4.3.3 : Rainfall (mm week^{-1}) and accumulated soil moisture deficit (mm).

S = weeks in which drought affected rate of transpiration.

4.3.1.5 Soluble nitrogen content of the soil

The amount of KCl - soluble nitrogen (NO_3^- and NH_4^+) in the soil was determined by the method of BREMNER (1965). Analyses were carried out on fresh samples and results expressed as parts per million (ppm) of soluble nitrogen in oven-dry soil.

Table 4.3.1 : Soluble nitrogen content of oven-dry soil, ppm N.

S.E. of 3 replicates is given in italics.

* Fertilizer treatments applied 6.5.74.

N1 = 0, N2 = 67, N3 = 135, N4 = 202 Kg N ha^{-1}

** Fertilizer treatments applied 23.8.74.

N1 = 22, N2 = 45, N3 = 67, N4 = 90 Kg N ha^{-1}

*** Compound fertilizer applied to all plots. 73 Kg N ha^{-1}

**** Fertilizer treatments applied 16.5.75

N1 = 0, N2 = 67, N3 = 135, N4 = 202 Kg N ha^{-1}

Date	Soil depth	Nitrogen treatment							
		N1		N2		N3		N4	
14.5.74 *	0 - 5 cm	24	*4*	75	*25*	146	*10*	237	*31*
	5 - 10 cm	23	*0*	23	*3*	53	*3*	52	*12*
14.6.74	0 - 5 cm	12	*2*	10	*1*	21	*5*	42	*13*
	5 - 10 cm	12	*1*	14	*1*	17	*3*	39	*14*
23.7.74	0 - 5 cm	8	*1*	7	*1*	14	*3*	9	*2*
	5 - 10 cm	11	*1*	13	*2*	13	*4*	9	*1*
9.9.74 **	0 - 5 cm	8	*1*	8	*1*	8	*0*	9	*1*
	5 - 10 cm	9	*1*	9	*0*	9	*0*	10	*1*
25.4.75 ***	0 - 5 cm	24	*7*					24	*7*
	5 - 10 cm	2	*1*					3	*1*
30.5.75 ****	0 - 5 cm	13	*1*	31	*6*			168	*52*
	5 - 10 cm	12	*2*	12	*0*			19	*2*
20.6.75	0 - 5 cm	3	*1*	4	*1*			32	*9*
	5 - 10 cm	5	*1*	4	*1*			20	*5*
12.7.75	0 - 5 cm	2	*0*	2	*0*			42	*9*
	5 - 10 cm	1	*0*	3	*0*			19	*4*

A low level of soluble nitrogen was measured in all plots only 2½ weeks after fertilizer application in August 1974. This was probably partly due to very heavy rainfall in the first week of September (see Section 4.3.1.4).

According to HENZELL & ROSS (1973), the amount of available nitrogen (nitrate, nitrite and ammonium) in the surface 15 to 30 cm of the soil is between 8 and 80 ppm. Nitrogen deficient soils contain only traces of nitrate and nitrite but up to 10 ppm of exchangeable ammonium. The two lowest nitrogen treatments appear to have been generally deficient in nitrogen, particularly in June and July 1975; the highest nitrogen treatment appears to have had a very low nitrogen content in 1974 only, from mid-summer onwards.

It is difficult to interpret soil-N measurements because the presence of soluble nitrogen is so transient. The amount present depends on the balance between additions (fertilizers and nitrification of organic matter) and removals (plant uptake, leaching and volatile losses) at any particular time.

4.3.2 LEAF TURNOVER

Dates of appearance and death of successive leaves on a tiller were recorded from May 9th 1974 (treatments N2, N3 and N4) or June 4th 1974 (treatment N1) until July 2nd 1975. Observations were made on vegetative tillers throughout the experiment, and on reproductive tillers in 1975.

The dates of appearance and death were used to calculate:

(i) time interval between appearance of successive leaves;

(ii) time interval between death of successive leaves;

(iii) leaf lifespan;

(iv) number of live leaves per tiller;

(v) relationship between the length of the leaf appearance interval and

(a) the concurrent leaf death interval,

(b) the leaf death interval one leaf appearance interval later;

(vi) mean ages of leaves at leaf positions 1 (youngest) to 7.

Calculations were carried out for vegetative and reproductive tillers separately.

Sampling Technique

Records were maintained on individual tillers until they died or were lost, when a fresh record was begun on an adjacent tiller. The observed tillers therefore tended to form, as time elapsed, a biased sample of the total population in terms of tiller age: new tillers were produced within the total population but not incorporated into the sampling population. The age discrepancy was removed whenever there was a widespread relabelling of tillers;

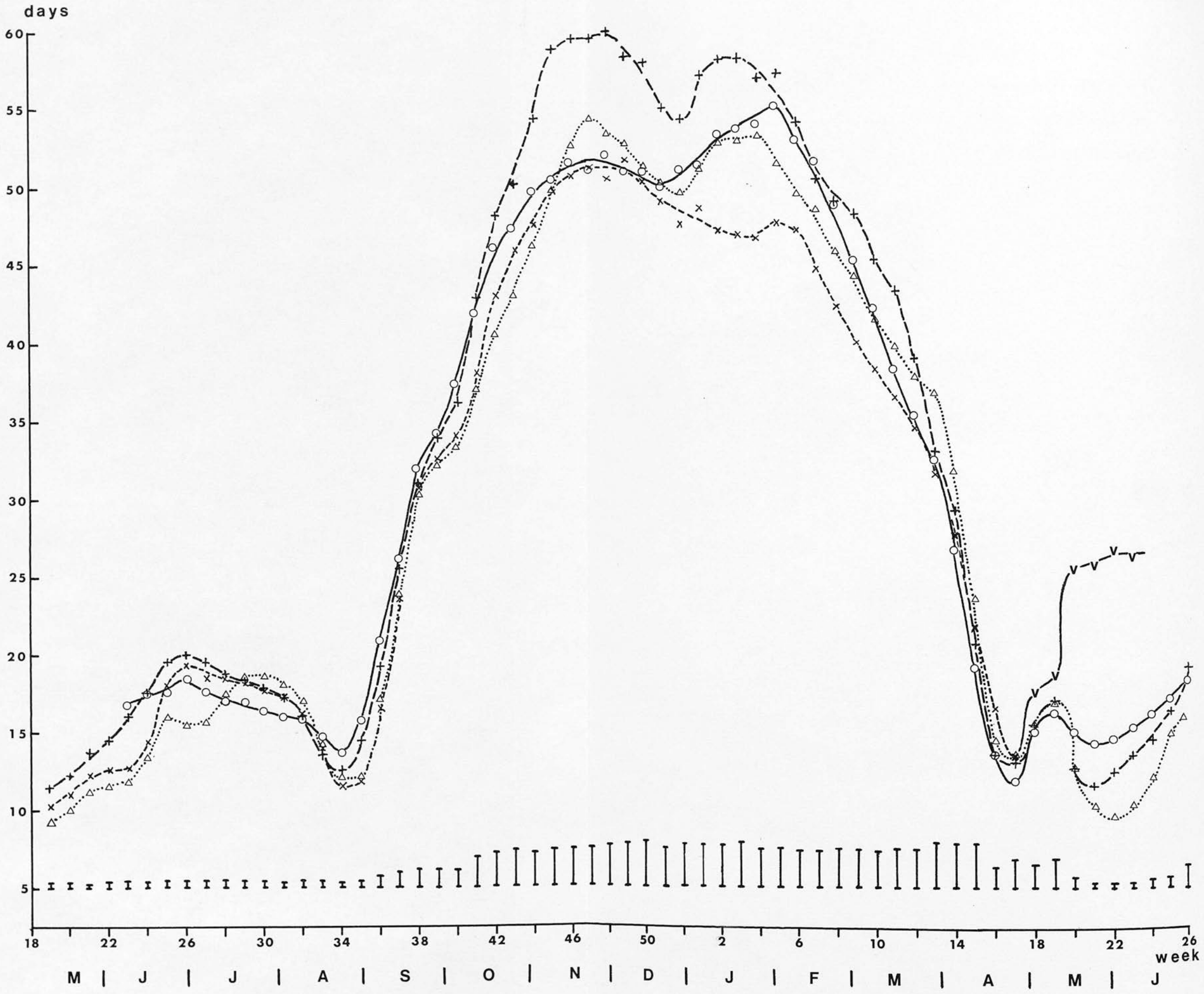
tillers were located within a limited area, but randomly with respect to age. Widespread re-labelling due to the loss or death of tillers took place after each cut.

Widespread re-labelling also took place during the period of reproductive development in 1975. At this time, if a labelled tiller developed signs of reproductive growth, a supplementary record was begun on the nearest apparently vegetative tiller whilst records on the old reproductive tiller were maintained. In early May 1975, 86% of marked tillers showed signs of reproductive development.

It is not possible to distinguish between reproductive and vegetative tillers during the early stages of growth following differentiation of the reproductive stem apex. Reproductive development in a tiller was suspected when the internodes began to lengthen and the number of live leaves increased to four or more. (It was at this stage that supplementary records were begun on apparently vegetative tillers). The reproductive state was confirmed only after jointing, flag leaf emergence (the flag leaf is rolled instead of folded), or head emergence. After the cut in May, many of the suspected-reproductive tillers were lost so their status was never clarified. In calculating results for the period prior to the cut, such tillers have been classified as vegetative.

For the purpose of calculation, a tiller classified as reproductive was placed in a separate category from the time at which the sixth leaf before ear emergence appeared; this was because during stem elongation and up until ear emergence the last five or six leaves to be produced by the tiller were usually

present and alive. Analysis of the results, however, showed that there was little difference between vegetative and reproductive tillers in terms of leaf appearance rate, leaf death rate and leaf lifespan until about three leaves before ear emergence.


days
60
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LEAF TURNOVER : VEGETATIVE TILLERS

4.3.2.1 Leaf appearance interval

The number of days between the appearance of successive leaves on a vegetative tiller are presented in Fig. 4.3.4 for each nitrogen treatment.

The leaf appearance interval remained steady for a considerable time during two periods of the year: from the end of April until the beginning of September (i.e. spring and summer) the mean appearance interval over all nitrogen treatments was 15 days. During September and October the interval lengthened rapidly until it levelled out again at about 1 leaf every 52 days from the end of October until the middle of February. From mid-February the interval shortened rapidly to the late spring and summer level.

Vegetative tillers growing in a reproductive sward

The leaf appearance interval (26 days) of vegetative tillers growing in an undefoliated sward dominated by reproductive tillers is indicated in Fig. 4.3.4 by the "V" symbols in weeks 20 to 23. The interval diverged rapidly and significantly from the leaf appearance interval (14.8 days) in a defoliated sward which had received the same no-nitrogen treatment in week 19 (N1 plots). The evidence in section 4.3.3.5a shows that most of the tillers growing in the defoliated N1 plots were vegetative. The interval of 14.8 days is therefore that of vegetative tillers growing in a largely vegetative sward.

Fig. 4.3.4. Days between successive leaf appearances under different nitrogen fertilizer treatments.

o——o = N1 +— —+ = N2

x- - - -x = N3 Δ·····Δ = N4

V——V = vegetative tillers growing in an undefoliated sward; see text.

Nitrogen fertilizer shortened the leaf appearance interval for six to eight weeks following its application. This effect is shown in Table 4.3.2 for the May 1974 and May 1975 applications of nitrogen.

Table 4.3.2 : Leaf appearance intervals following May applications of nitrogen fertilizer. S.E. given in italics. (days)

1974

No. of weeks after application	Kg N ha^{-1} 0	67	135	202
1	-	11.4 ± *0.4*	10.1 ± *0.4*	9.3 ± *0.3*
3	-	13.7 ± *0.3*	12.1 ± *0.3*	11.2 ± *0.3*
5	16.8 ± *0.6*	16.0 ± *0.4*	12.7 ± *0.3*	11.8 ± *0.4*
7	17.8 ± *0.5*	19.4 ± *0.5*	17.9 ± *0.6*	15.9 ± *0.6*

1975

No. of weeks after application	Kg N ha^{-1} 0	67	135	202
1	14.7 ± *0.6*	12.1 ± *0.6*	-	11.6 ± *0.6*
3	14.8 ± *0.4*	12.9 ± *0.4*	-	9.8 ± *0.4*
5	16.5 ± *0.6*	15.4 ± *0.5*	-	13.2 ± *0.6*
6	17.7 ± *0.8*	17.5 ± *1.1*	-	15.0 ± *1.0*

The effect of ~~increasing~~ applying N was to bring about an immediate reduction in leaf appearance interval. The effect became progressively less marked so that after 7 weeks only the highest N treatment was still showing an enhanced rate of leaf appearance relative to the no-nitrogen treatment.

Leaf appearance interval was also shortened following nitrogen fertilizer application in August 1974, as is shown in Table 4.3.3. The effect was greatest in the highest nitrogen treatment and had almost disappeared within 5 weeks of fertilizer application.

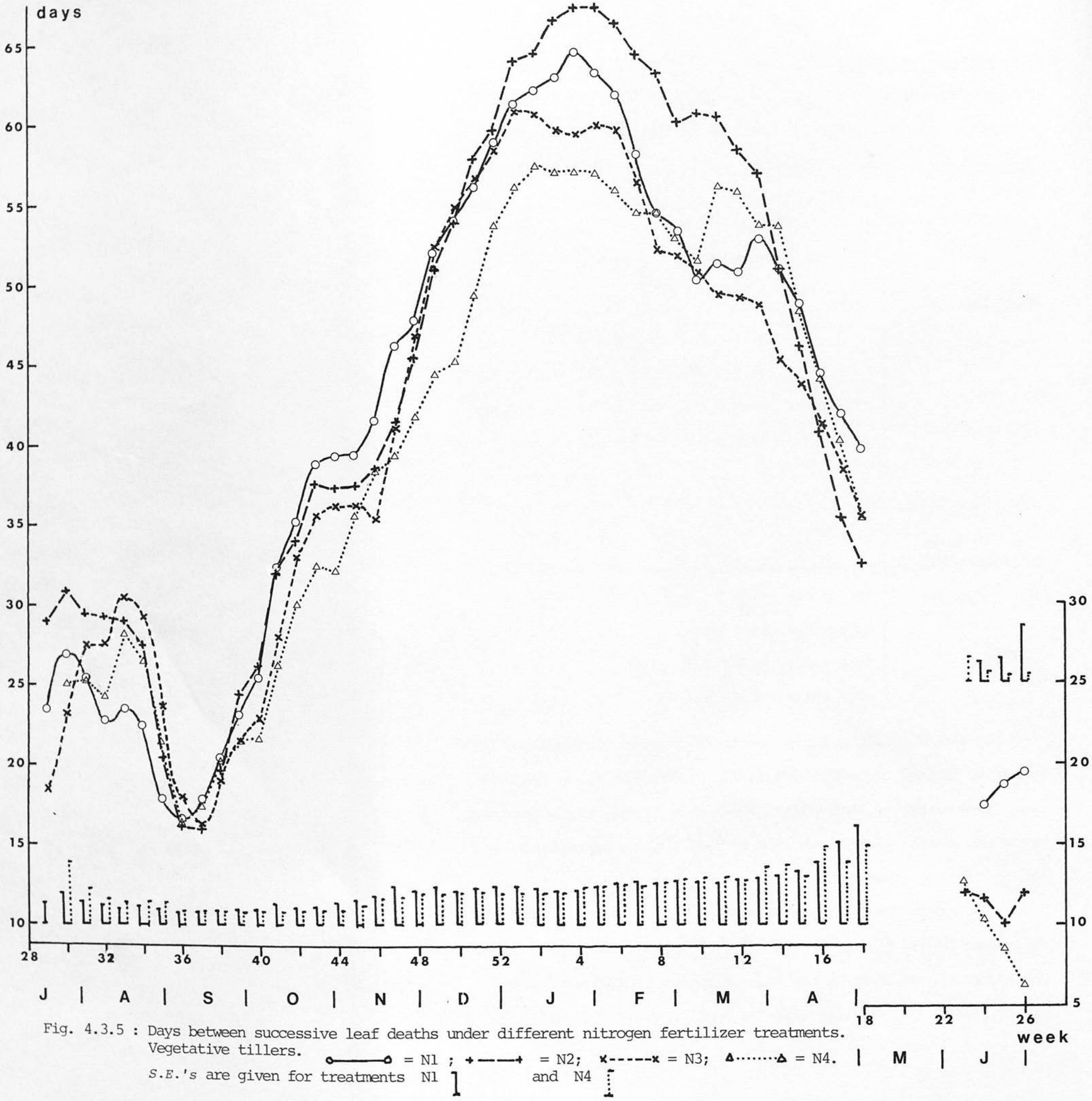


Fig. 4.3.5 : Days between successive leaf deaths under different nitrogen fertilizer treatments. Vegetative tillers. ○——○ = N1 ; +——+ = N2; ×-----× = N3; △·····△ = N4.
S.E.'s are given for treatments N1] and N4]

Table 4.3.3 : Leaf appearance intervals following August application of nitrogen fertilizer, 1974. S.E. given in italics.

No. of weeks after application	(days) Kg N ha^{-1} 22	45	67	90
1	14.8 ± *0.5*	13.5 ± *0.5*	11.7 ± *0.3*	12.1 ± *0.4*
3	23.6 ± *1.1*	22.3 ± *1.0*	20.1 ± *0.9*	20.4 ± *0.8*
5	33.1 ± *1.2*	32.5 ± *1.2*	31.7 ± *1.0*	31.2 ± *1.0*

It will be recalled that there was very little soluble-nitrogen left in the soil only 2½ weeks after its application in August, possibly due to heavy rain in the 2nd week (section 4.3.1.5).

4.3.2.2 Leaf death interval

Leaf death interval is the number of days between successive leaf deaths on a tiller; leaves almost always die in chronological order. Death of a leaf was defined as the complete loss of green colouration. Fig. 4.3.5 shows the leaf death interval from July 22nd 1974 to July 1st 1975 under each nitrogen treatment.

During July and August 1974 leaves were dying at the rate of about 1 leaf every 26 days. In early and mid-September there was a sharp increase in the rate of leaf death to about 1 leaf in every 17 days. The interval between leaf deaths then lengthened steadily to a maximum, over all nitrogen treatments, of about 61 days in late January 1975. Thereafter it declined again to approximately 13 days in the latter half of June. There were signs that the interval was beginning to lengthen again in the two lowest nitrogen treatments at the end of June. Standard errors are very large in May and early June 1975 because so many of the marked tillers became reproductive or were lost during the cut in May and new tiller records had to be begun.

Nitrogen fertilizer

Differences in leaf death interval between nitrogen treatments are shown in Table 4.3.4.

Table 4.3.4 : Effect of applied nitrogen on leaf death interval (days). Vegetative tillers. S.E. of mean is in italics.

N treatment	1974 Week 34	37	43	49	1975 Week 3	9	15	23	25
N1	22.6	17.9	37.4	51.7	62.5	53.0	48.6	23.1	18.8
	1.3	*0.9*	*1.2*	*2.4*	*2.2*	*2.8*	*3.4*	*4.2*	*1.7*
N2	27.6	15.9	37.5	50.7	66.1	59.7	45.8	11.9	10.1
	1.5	*0.9*	*1.1*	*2.5*	*2.3*	*3.2*	*4.8*	*1.1*	*1.0*
N3	29.3	16.3	35.5	52.1	59.2	51.4	43.4		
	1.5	*1.0*	*1.4*	*2.6*	*2.2*	*2.3*	*2.3*		
N4	26.6	17.4	32.3	44.2	56.7	52.5	48.0	12.7	8.4
	1.6	*1.0*	*1.0*	*2.1*	*2.0*	*3.1*	*3.3*	*1.6*	*0.5*
Significance	N.S.	N.S.	**	**	*	N.S.	N.S.	*	***

In general, larger amounts of nitrogen fertilizer applied in week 34, August 1974, shortened the leaf death interval in weeks 43, 49 and 3; it was only in the highest nitrogen treatment that the effect was consistently significant.

The shorter death interval observed in weeks 43, 49 and 3 was from leaves which appeared in weeks 34, 38 and 41. It was in week 34 that the fertilizer treatments were applied and it has already been shown (section 4.3.2.1, p.121) that in the following four to six weeks the leaf appearance interval differed between treatments. The leaf death intervals in weeks 43 to 3 must therefore correspond to an effect of nitrogen on the lifespans of those leaves produced shortly after its application in week 34.

In May 1975, following another application of nitrogen fertilizer in week 19 (N1 = 0, N2 = 67, N4 = 202 Kg N ha^{-1}), leaf death interval once again differed significantly between treatment levels. In week 19 there was no difference; four weeks later leaves in treatments N2 and N4 were dying faster than in N1 ($P < 0.05$), and two weeks later still in week 25 the difference had become highly significant ($P < 0.001$). N2 and N4 had begun to diverge but the difference had not quite reached the level of significance by the end of the experiment in week 26. The highest level of nitrogen applied appeared to be leading to a still faster rate of leaf death while in treatment N3 the response was disappearing.

Leaves that died in weeks 23 and 25 appeared in weeks 17 and 18 respectively (i.e. before fertilizer was applied). Since nitrogen had a significant effect on leaf death rate in weeks 23 and 25, it would appear that at this time of year nitrogen also affected the rate of senescence of younger leaves already present when the fertilizer was applied.

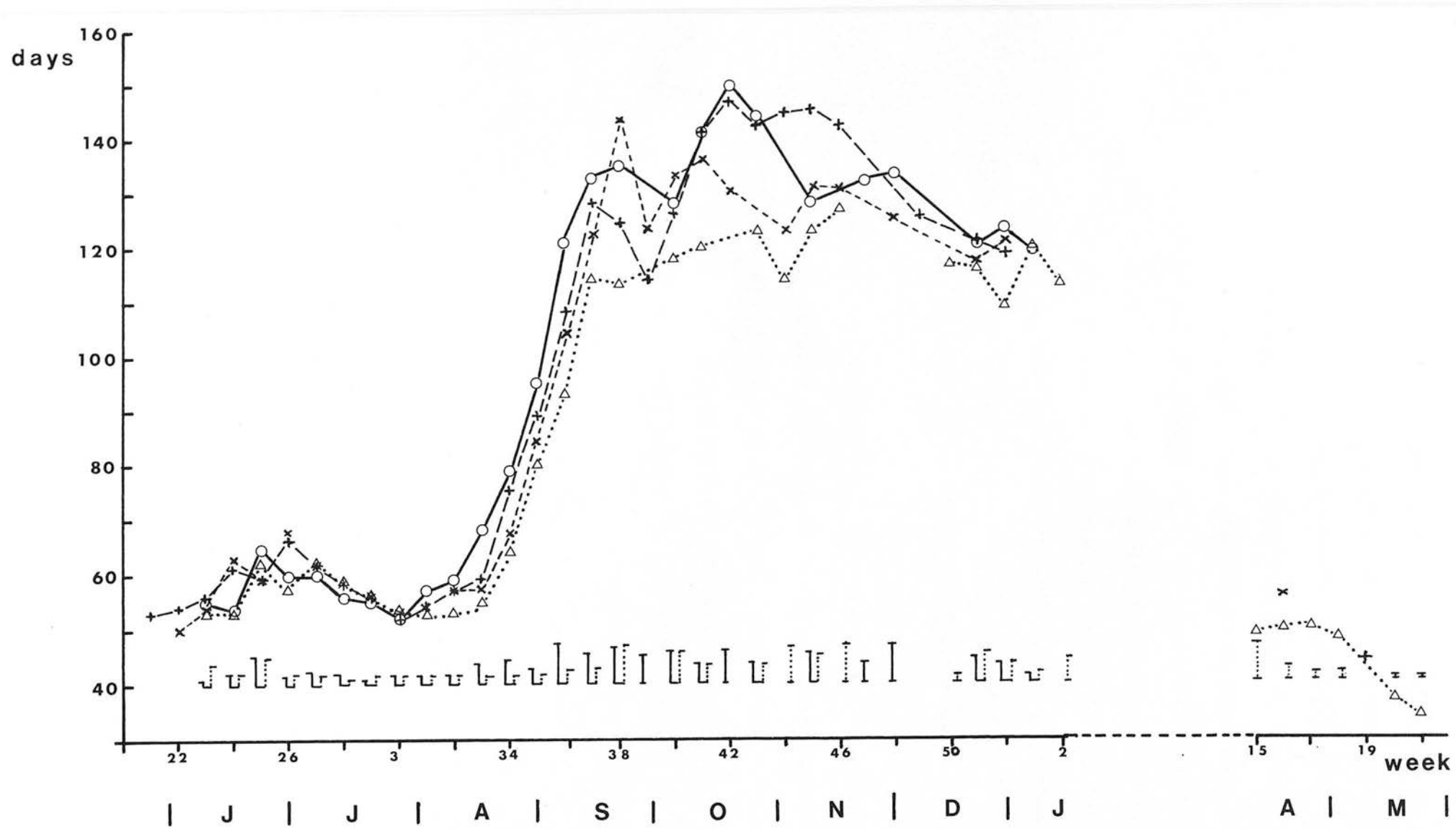


Fig. 4.3.6 : Lifespan of leaves appearing in successive weeks of the year. Vegetative tillers.

o——o = N1 ; +— —+ = N2 ; ×- - - -× = N3 ; Δ····· Δ = N4 .

S.E.'s are given for treatments N1 I and N4 I

4.3.2.3 Leaf lifespan

Leaf lifespan is the number of days between the appearance of a leaf and its subsequent death. It was calculated by subtracting the date of death from the date of appearance of every leaf that had been observed throughout the whole of its lifespan. The average lifespan of all leaves appearing in a given week is plotted in Fig. 4.3.6 for each nitrogen treatment.

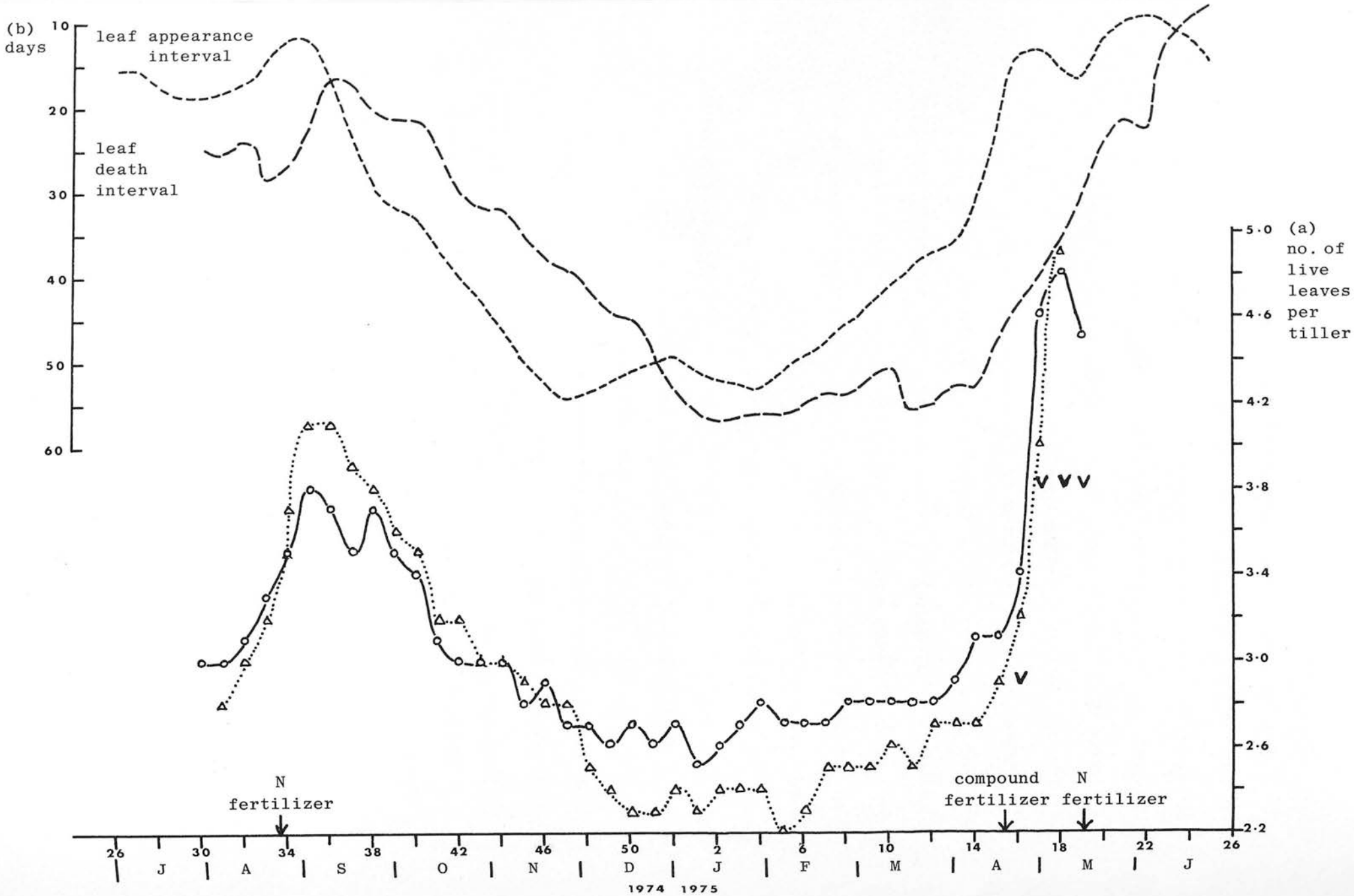
Standard errors are large partly because tiller loss or reproductive development reduced the number of vegetative leaves followed through from appearance to death. The variation is also in part due to a naturally wide range in lifespan of leaves appearing on one date, leading to groups of tillers bearing two, three, four or five live leaves per tiller.

As with leaf appearance interval, there were two marked plateaus in leaf lifespan during the year. Leaves appearing between June and mid-August 1974 lived for 50 to 60 days whereas those appearing between mid-September and January lived for 120 to 140 days. The lifespan increased from 55 to 130 days within a very short space of time, between mid-August and mid-September.

Nitrogen fertilizer

Nitrogen was found to shorten the lifespan of leaves in correspondence with its effect of ~~reducing~~ increasing both the leaf appearance rate and the leaf death rate of the same set of leaves.

An increase in the level of nitrogen applied significantly ($P < 0.05$) reduced the lifespan of leaves that appeared in the first 4 weeks following its application on 23rd August 1974 (week 34). Leaves appearing in week 34 lived 64 days under the highest nitrogen treatment (N4) and 78 days under the lowest (N1). Those appearing


(b)
days
10
20
30
40
50
60
leaf appearance interval
leaf death interval
(a)
no. of live leaves per tiller
5·0
4·6
4·2
3·8
3·4
3·0
2·6
2·2
N fertilizer
compound fertilizer
N fertilizer
26
30
34
38
42
46
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1974
1975

in week 37 lived 114 and 133 days respectively. By week 43 only the highest nitrogen treatment had an effect on leaf lifespan (123 days compared with 143 days in the other treatments; $P < 0.05$).

4.3.2.4 Number of live leaves per tiller

Leaves were regarded as alive until they had turned 100% brown. The numbers of live leaves on each tiller were not counted directly but were extracted from the leaf appearance and death records. The calculation could only be done if the date had been recorded on which the previous leaf in the succession had died. Not many natural leaf deaths (as opposed to removal by defoliation) occurred before July 1974.

The number of live leaves per tiller throughout the year is plotted in Fig. 4.3.7, for the lowest (N1) and highest (N4) nitrogen treatments. Superimposed on the graph are the leaf appearance and leaf death intervals of treatment N4. When leaves appeared faster than older leaves were dying, the number of live leaves per tiller increased, and vice versa.

Fig. 4.3.7 : (a) Number of live leaves per tiller on the lowest (N1) and highest (N4) nitrogen treatments.

o——o = treatment N1

Δ·····Δ = treatment N4

The "V"s represent the number of live leaves per tiller on purely vegetative tillers growing in mixed swards of reproductive and vegetative tillers before cutting.

(b) Leaf appearance interval and Leaf death interval under the highest (N4) nitrogen treatment.

- - - - - - - = leaf appearance interval

——— = leaf death interval

During the winter the number fell to a constant level of 2.7 (N1) and 2.4 (N4) even though leaf appearance intervals and leaf death intervals were not the same. Differences between the intervals were, however, small in relation to their total lengths.

The number of live leaves per tiller rose to a peak in August 1974 and May 1975. The tillers observed in August 1974 were definitely vegetative although there were reproductive tillers present in the sward; those tillers observed in May 1975 included reproductive ones (see section 4.3.2 on sampling technique).

There is evidence that the apparently high number of live leaves per tiller in weeks 17 to 19 1975 arose from the inclusion of "suspected-reproductive' tillers in the calculations for treatments N1, N2 and N4. Thus in the N3 treatment plots, where the vegetative or reproductive status of every marked tiller was eventually determined, the calculation of number of live leaves per tiller was carried out on purely vegetative tillers. The values are represented by "V"s in Fig. 4.3.7. The average number of live leaves per tiller on definitely vegetative tillers was similar to that calculated for mixed sampling populations of vegetative and reproductive tillers up until week 16. The average number of live leaves on vegetative tillers then increased quickly, but up to a maximum of only 3.8 live leaves per tiller as compared to about 4.6 in the mixed sampling populations.

The number of live leaves on vegetative tillers therefore appears to have ranged between about 2.4 in winter to 3.9 during times of reproductive stem elongation.

Nitrogen fertilizer treatments had little effect on live leaf number per tiller, a significant effect only being found in week 37 shortly after fertilizer application, when N1 carried fewer live leaves (3.47) than N2, N3 or N4 (3.99) ($P < 0.05$). At this time the higher levels of nitrogen fertilizer were causing increased rates of leaf appearance but not death (see sections 4.3.2.1 and 4.3.2.2). From week 2 to week 7 treatments N3 and N4 consistently bore fewer live leaves per tiller (2.3) than N1 and N2 (2.6). The difference is related to the faster death rate of leaves under high nitrogen treatments at this time.

4.3.2.5 Relationship between leaf death intervals and leaf appearance intervals.

In Figure 4.3.7 the appearance intervals and death intervals of leaves in the highest nitrogen treatment (N4) are shown together. The pattern of change in leaf death interval is remarkably similar to that in leaf appearance interval but lags behind by an amount varying from 21 days in May and June 1975 to 56 - 70 days in December to March, *viz* by about 1 leaf appearance interval. A strong correlation was found between leaf death interval and the preceding leaf appearance interval ($r = 0.94$, $P < 0.001$). There was also a correlation between the lengths of the leaf death interval and leaf appearance interval in the same week ($r = 0.72$, $P < 0.001$) but the relationship was not so strong.

There is generally one expanding, one mature, and one senescing leaf on a tiller. The leaf appearance interval is approximately equal to the time taken for the growing leaf to expand to mature size; the leaf death interval represents the rate of senescence of the oldest leaf. The correlation coefficients suggest, therefore,

that rate of senescence of the oldest leaf is less dependent on current environmental conditions governing growth, than on the previous conditions it experienced when it was the mature leaf.

4.3.2.6 Leaf age

The mean ages of each of the last seven leaves to appear were calculated for every week under each nitrogen treatment. They are used to calculate the rates of change in digestibility, weight and height of individual leaves as they grow older.

The values actually used for each nitrogen treatment are given in Appendix 5, but a summary of averages over nitrogen treatments is given here.

Table 4.3.5 : Ages (in days) of the youngest (1st) to oldest leaves on a vegetative tiller, averaged over all nitrogen treatments.

Sward Sampling Date	Leaf position			
	1	2	3	4
24.5.74	4	-	-	-
24.6.74	8	19	30	-
14.8.74	9	26	42	56
2.10.74	13	28	39	55
6.11.74	22	51	64	77
16.12.74	33	74	97	109
18.1.75	22	71	110	132
4.3.75	26	74	122	161
4.4.75	22	68	115	159
4.5.75	6	20	45	84
4.6.75	6	20	-	-
3.7.75	10	23	31	39

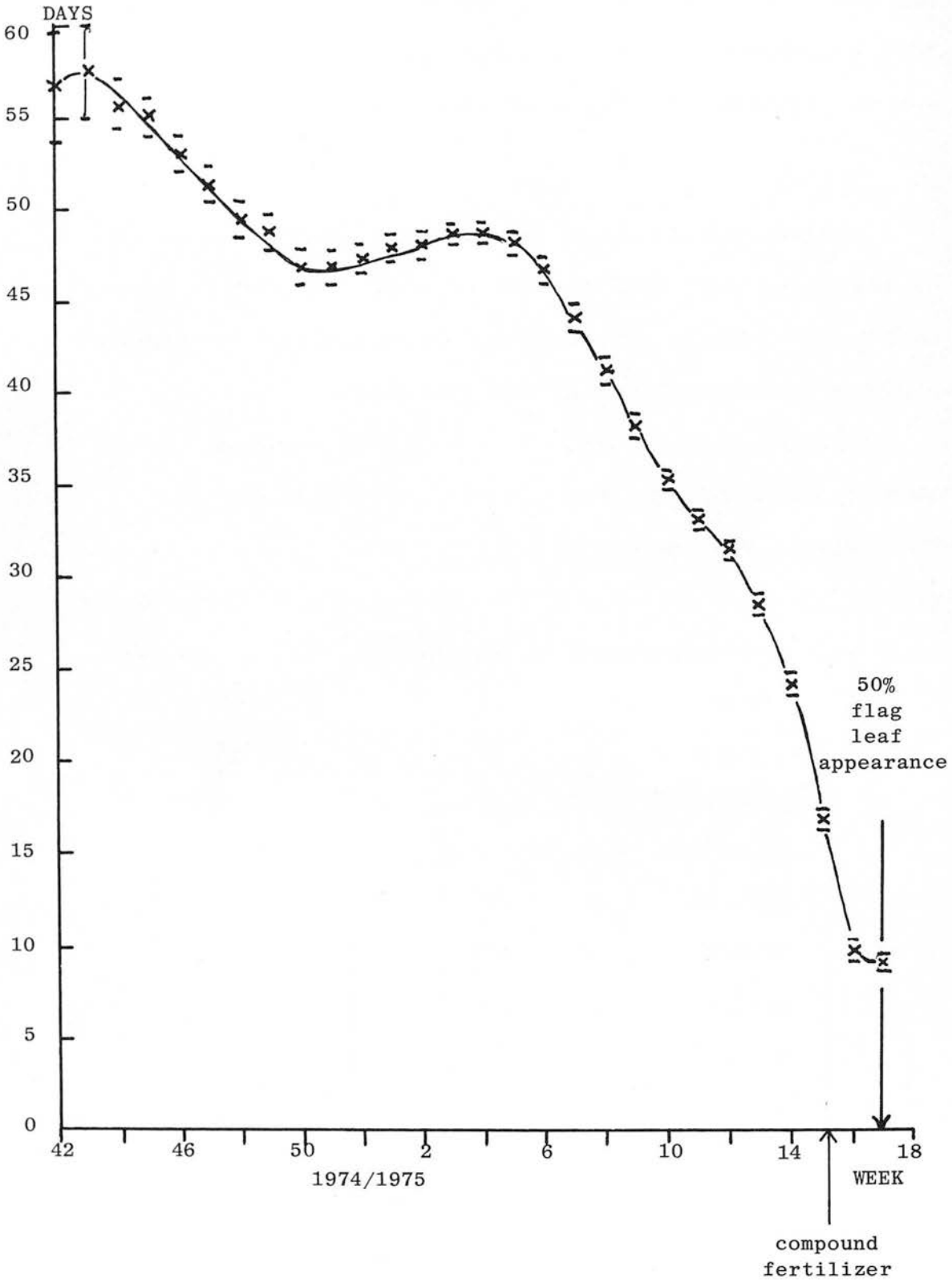


Fig. 4.3.8 : Leaf appearance interval,

Reproductive Tillers in uncut swards.

I S.E.

REPRODUCTIVE TILLERS

Leaf turnover and head emergence on reproductive tillers was recorded in 1975 in uncut plots. Observations were made in all plots up to week 19. On 17th April (week 16), 250 Kg ha^{-1} of compound fertilizer 29-5-5 was applied to the whole area.

On May 15th 1975 (week 20) the N1, N2 and N4 plots were cut; records of reproductive tiller development were continued on two of the remaining uncut plots (formerly N3 plots) to which no further fertilizer was applied.

4.3.2.7 Leaf appearance interval (Fig. 4.3.8)

The leaf appearance interval on reproductive tillers was the same as that on vegetative tillers up until week 16 (mid-April). The penultimate and flag leaves emerged on almost all the reproductive tillers in weeks 16 to 18.

There was no residual effect of nitrogen on leaf appearance interval from treatments applied the year before.

"Stem" thickening and sheath elongation above the previous sheath were observed in some tillers as early as week 11 (mid-March).

4.3.2.8 Emergence of flag leaf and flowering head (Fig. 4.3.9)

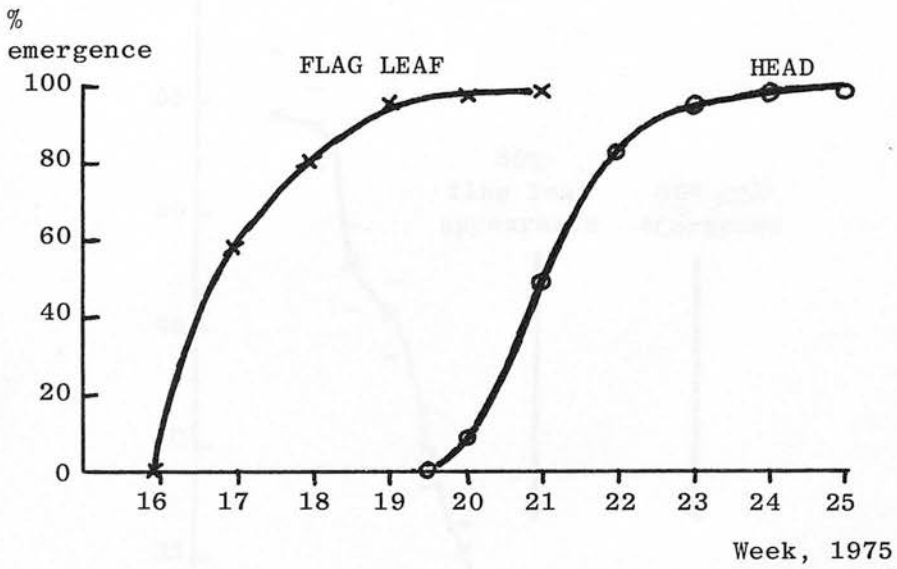


Fig. 4.3.9 : Percentage emergence of flag leaf and flowering head on reproductive tillers.

The flag leaf emerged on almost all reproductive tillers (80%) within a short space of time from the middle of week 17 (26th April) to the middle of week 18 (3rd May). The mean date of emergence was 24th April ± 0.5 days, which was 6.8 ± 0.4 days after emergence of the penultimate leaf.

Ear emergence followed four weeks later, most ears (72%) emerging in weeks 21 and 22. 50% ear emergence had occurred by May 26th.

4.3.2.9 Leaf death interval (Fig. 4.3.10)

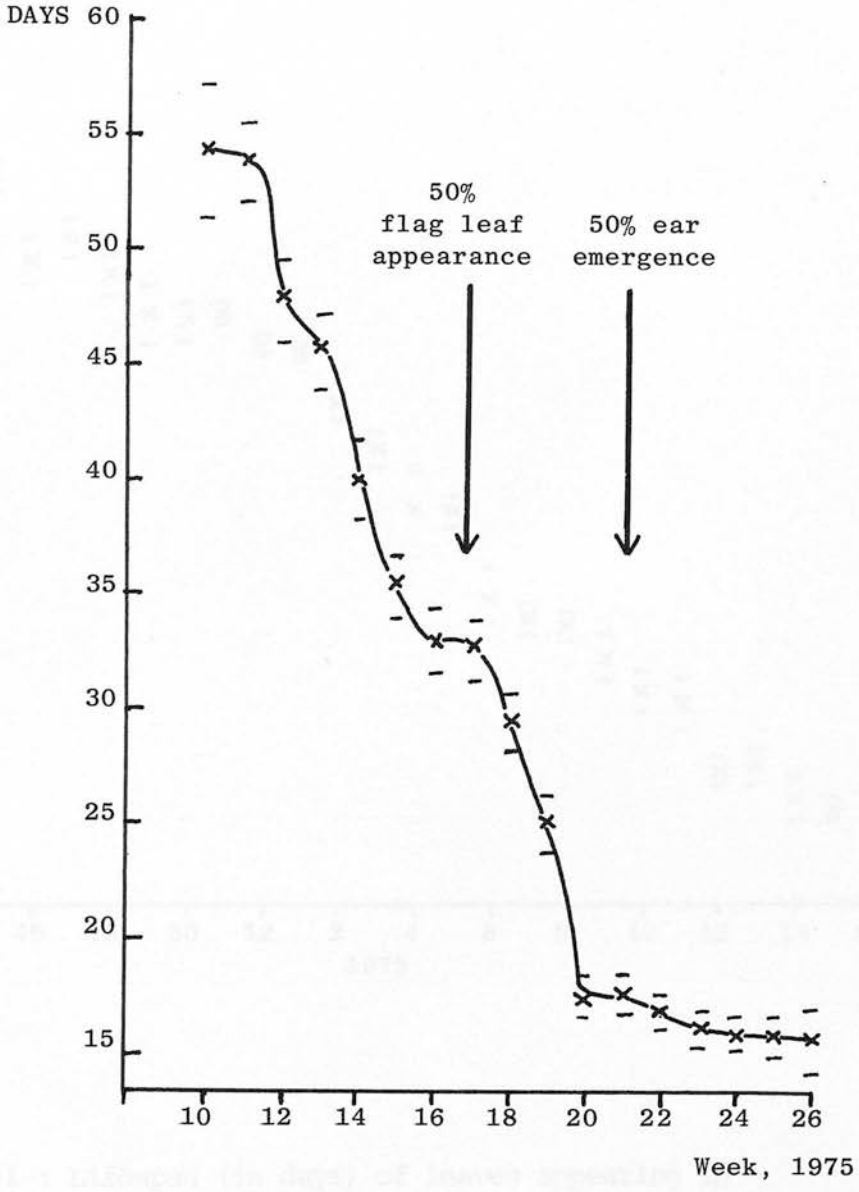


Fig. 4.3.10 : Number of days between successive leaf deaths on reproductive tillers.

The number of days between successive leaf deaths was consistently 5 - 10 days shorter in reproductive than in vegetative tillers from week 14 until week 20. After week 20 the rate of leaf death became constant at 1 leaf every 16 days.

4.3.2.10 Leaf Lifespan (Fig. 4.3.11)

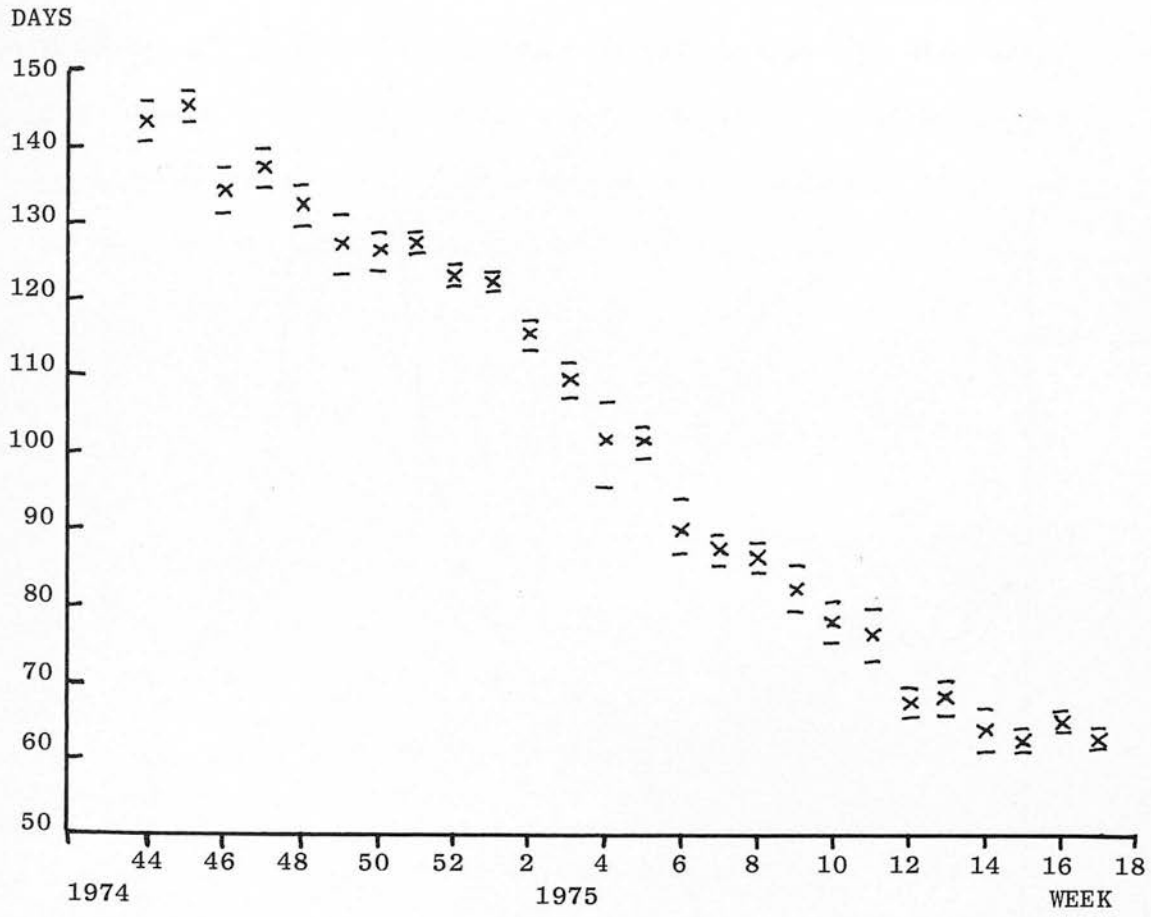


Fig. 4.3.11 : Lifespan (in days) of leaves appearing in weeks 44 to 17. Reproductive tillers.

Leaf lifespan decreased at a linear rate from 145 days for leaves appearing in week 44 (early November) to 64 days for leaves appearing in week 14 (early April). A leaf which appeared in early November generally became the 6th oldest leaf on a reproductive tiller after ear emergence. A leaf appearing in early April was generally the 3rd or 2nd last leaf to appear before ear emergence.

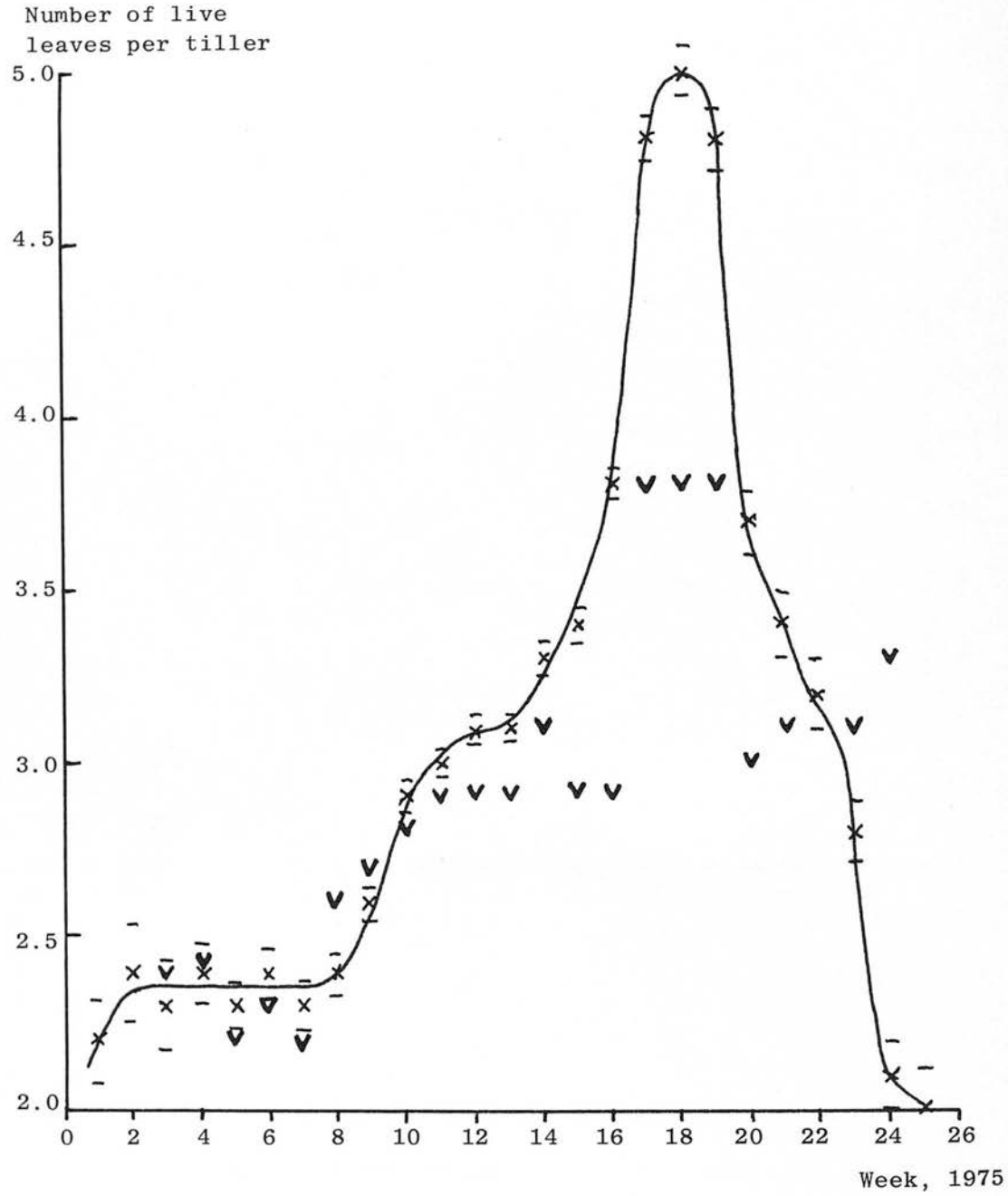


Fig. 4.3.12 : Number of live leaves per tiller, reproductive tillers. The "V"s represent the number of live leaves per tiller on purely vegetative tillers growing in uncut mixed swards of reproductive and vegetative tillers (see section 4.3.2.4).

4.3.2.11 Number of live leaves per tiller (Fig. 4.3.12)

The number of live leaves on reproductive tillers was similar to that on vegetative tillers up until week 16 (3.8 live leaves per tiller), after which it increased to 5.0 in week 18. The number then fell at a fairly constant rapid rate while the older leaves were dying and no further leaves were being produced. From week 20 onwards, leaves were dying at a constant rate.

4.3.3 STRUCTURE OF THE SWARD

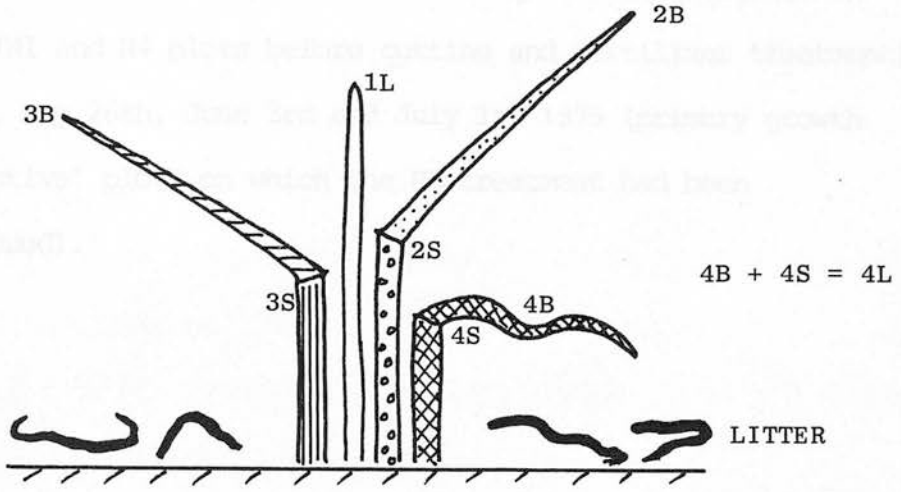


Fig. 4.3.13 : Fractions into which the sward was separated.

The structure of the sward was analysed in terms of the heights, weights and digestibilities of its constituent parts. The fractions into which the sward was divided were the different parts of the vegetative tiller : 1st leaf (1L); 2nd blade (2B) and second sheath (2S); 3rd blade (3B) and third sheath (3S); 4th blade (4B) and 4th sheath (4S) - usually bulked as 4th leaf (4L) to give sufficient dry weight of material for digestibility analysis; Loose standing litter was also taken into account. Tiller samples were cut at ground level.

Sampling took place at intervals throughout the year. All nitrogen treatment plots were sampled on June 24th, August 14th, October 2nd, November 6th, December 14th 1974. Only N1 and N4 plots were sampled on January 18th, March 4th, April 4th and May 4th 1975. Following a further application of fertilizer treatments in May 1975, sward structure was examined in the N1, N2 and N4 plots. Any reproductive tillers were removed from the tiller samples and their structure analysed separately. Tillers were classified as reproductive if a joint was found when the leaves were peeled away.

N1, N2 and N4 plots were sampled on June 4th and July 4th.

The structure of reproductive tillers was investigated on May 6th (N1 and N4 plots before cutting and fertilizer treatment), May 21st, May 26th, June 3rd and July 1st 1975 (primary growth 'reproductive' plots on which the N3 treatment had been discontinued).

4.3.3.1 DIGESTIBILITIES OF PLANT PARTS

In Vitro Organic Matter Digestibility (IVOMD) was calculated as the percentage of organic matter digested per unit weight of organic matter.

VEGETATIVE TILLERS

IVOMD of whole tillers from December 1974 to July 1975 is shown in Table 4.3.6, averaged over all nitrogen treatments.

Table 4.3.6 : IVOMD of vegetative tillers averaged over all nitrogen treatments. Mean ± S.E.

	Date						
	17.12.74	18.1.75	4.3.75	4.4.75	4.5.75	4.6.75	4.7.75
Mean	61.0	58.1	55.6	69.8	79.7	76.7	76.2
S.E.	*1.5*	*0.8*	*1.5*	*0.8*	*1.6*	*0.8*	*0.5*

(a) Seasonal changes in digestibilities of leaf blades and sheaths

The O.M. digestibilities of the 1st leaf, 2nd and 3rd blades, 4th leaf and standing litter are shown in Fig. 4.3.14. The values presented are averages over all nitrogen treatments except where Analysis of Variance showed nitrogen to have had a significant effect on digestibility; in such cases the value for the lowest (N1) treatment is given.

Digestibilities of the second and third sheaths are presented separately in Fig. 4.3.15.

In describing the results, those of July 1975 are considered separately; they are anomalous and coincide with a severe drought stress.

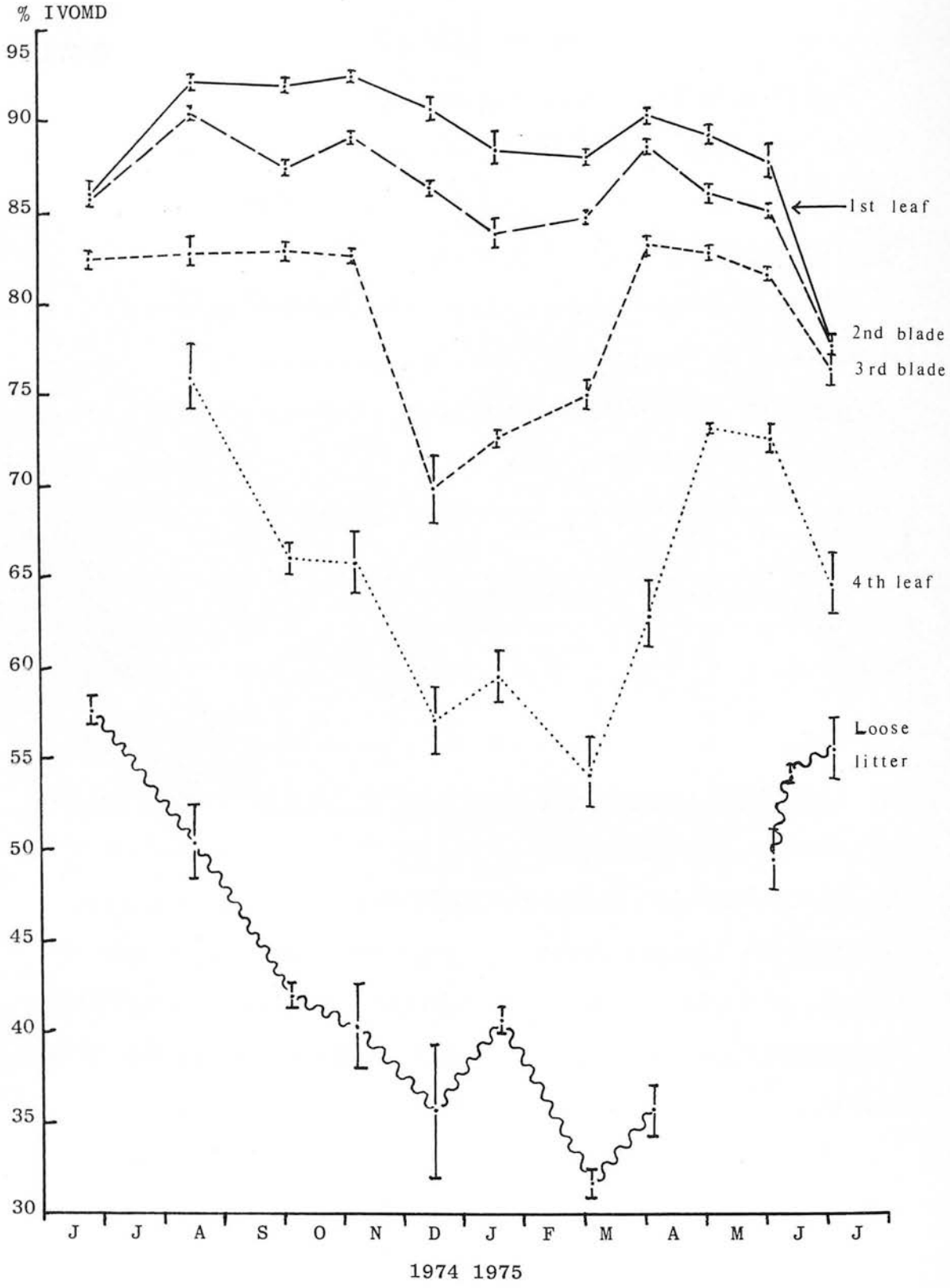


Fig. 4.3.14 : *In vitro* organic matter digestibilities of parts of the vegetative tiller. Values have been averaged over all nitrogen treatments except where nitrogen had an effect on the digestibility. In such instances, the value for the lowest nitrogen treatment, N1, has been taken.

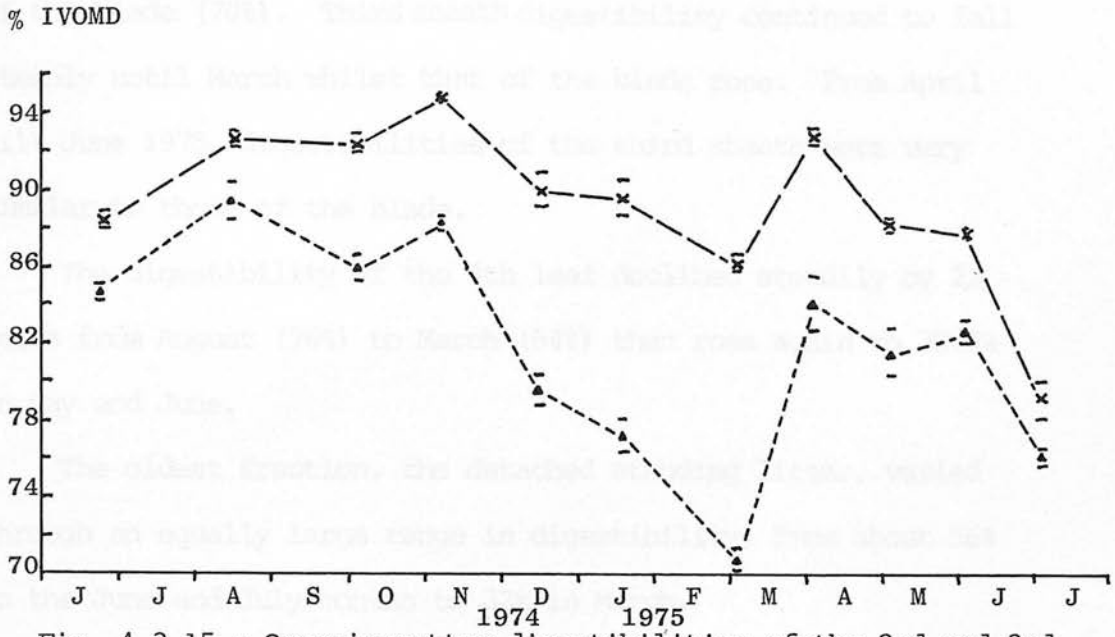


Fig. 4.3.15 : Organic matter digestibilities of the 2nd and 3rd sheaths, averaged over all nitrogen treatments.

– – – 2nd sheath ---- 3rd sheath

Digestibilities of the 1st leaf, 2nd blade and 2nd sheath varied within fairly small ranges of 6 to 8 units during the year. Lowest values were in June 1974, January, March and June 1975. The 1st leaf, (mean digestibility over the year: 89%), was 0 to 4 units higher in digestibility than the 2nd blade (mean: 86%) during the year; and the 2nd sheath (mean: 90%) was always 3 to 6 units higher than the blade.

The digestibility of the third blade was fairly constant at about 82.5% from June to November and April to June. It fell 13 units between early November and mid-December, and remained low for the rest of the winter at around 70 to 75%. The third sheath was 2 to 6 units higher in digestibility than the blade from June to November (mean: 87%); its digestibility then fell rapidly by about 8 units to 79.5% in December but it was still much higher than that

of the blade (70%). Third sheath digestibility continued to fall steeply until March whilst that of the blade rose. From April till June 1975, digestibilities of the third sheath were very similar to those of the blade.

The digestibility of the 4th leaf declined steadily by 22 units from August (76%) to March (54%) then rose again to 72.5% in May and June.

The oldest fraction, the detached standing litter, varied through an equally large range in digestibility, from about 56% in the June and July months to 32% in March.

It should be noted that, in general, the digestibilities of the three youngest leaves were relatively high and constant from April to November and fell in the winter. The digestibility of the 3rd leaf was markedly lower in winter, possibly corresponding to the fall in the number of live leaves per tiller during this period to about 2.6. Furthermore, the 4th leaf only had a digestibility above 70% in August 1974 and May to June 1975 - both times when the number of live leaves per tiller rose to peaks of 3.8 or 4.0.

(b) Effect of nitrogen on digestibility

Nitrogen tended to reduce the digestibility of leaves in the 1st and 2nd leaf positions by 2 to 4 units in the first few weeks following nitrogen fertilizer application, but the effect seldom reached the 5% level of significance.

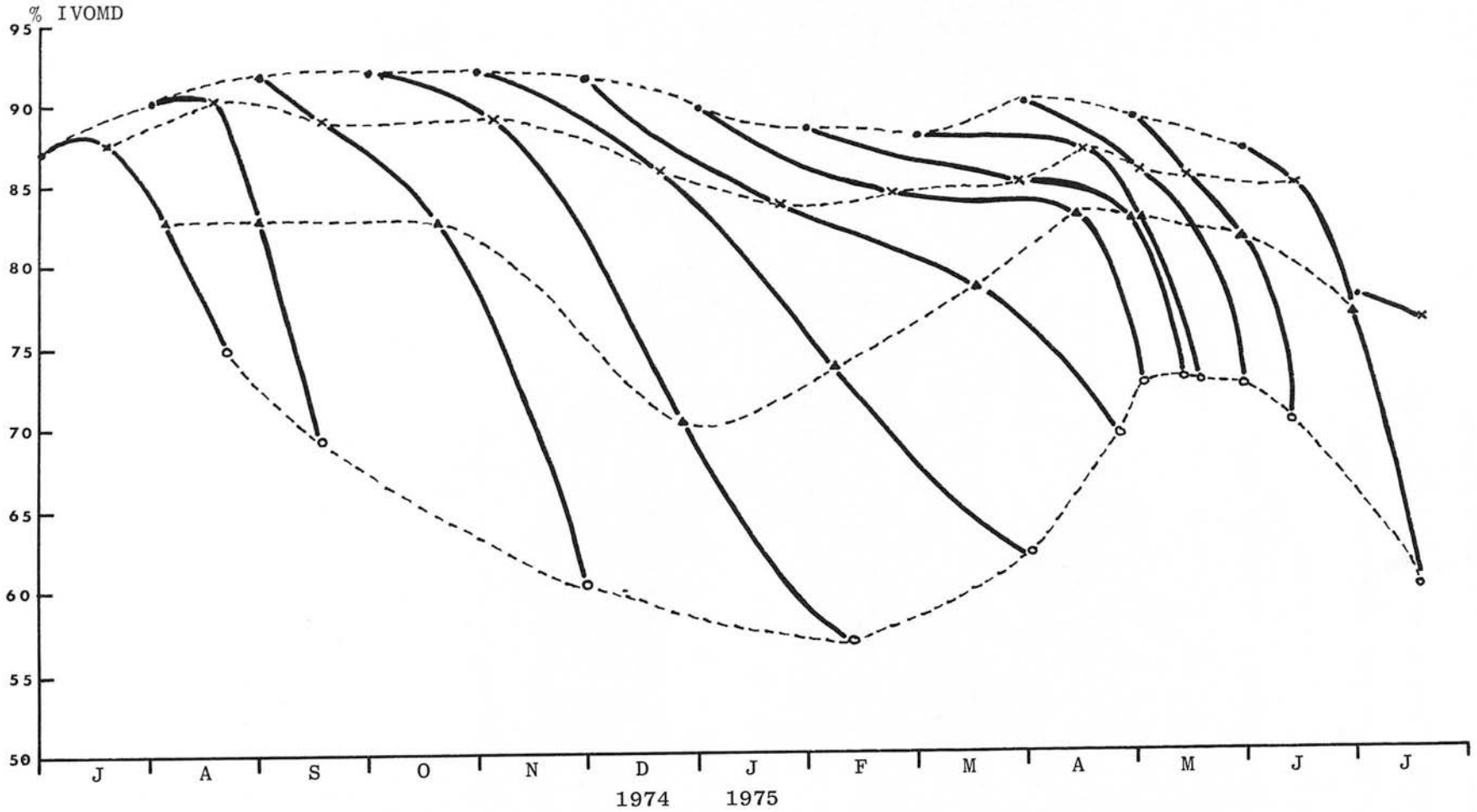


Fig. 4.3.16 : Change in digestibility of an individual leaf as it grows older.

Starting points are half-emerged leaves on the first day of each month.

——— digestibility of an individual leaf as it grows older.

----- digestibility of leaves at a particular leaf position.

• = 1L × = 2B ▲ = 3B o = 4L

During the period of water stress in June and July 1975, however, the youngest leaf (1L) growing in the two lowest nitrogen treatments (N1 and N2) was much less digestible than the emerging leaf in the N4 plots.

O.M. digestibility 4.7.75	N1	N2	N4
1st leaf, mean	77.3	78.7	83.8
S.E.	±0.6	±0.6	±0.4

(c) Changes in digestibility as leaves age

Fig. 4.3.16 shows the changing digestibility of individual leaves as they aged. The pattern has been worked out for a new leaf each month. The 1L fraction in the tiller separations contained leaves varying in age from leaf tip just emerged to blade almost fully expanded. The mean age of the fraction was therefore one-half of a leaf appearance interval; and the digestibility of the fraction was therefore the digestibility of leaves which were, on average, ½ a leaf appearance interval old. Similar reasoning shows that the digestibility of the 2nd blade was that of blades whose mean age was 1½ leaf appearance intervals; that of the 3rd blade corresponded to an age of 2½ leaf appearance intervals; and that of the 4th leaf to 3½ intervals.

The information used in the construction of these relationships was derived from Fig. 4.3.14 (O.M. digestibilities of the parts of a vegetative tiller) and from Fig. 4.3.4 (leaf appearance intervals).

The digestibility of a half-emerged leaf on the first day of a month was obtained from Fig. 4.3.14 as being equal to the digestibility of the 1L fraction on that day. One leaf appearance interval

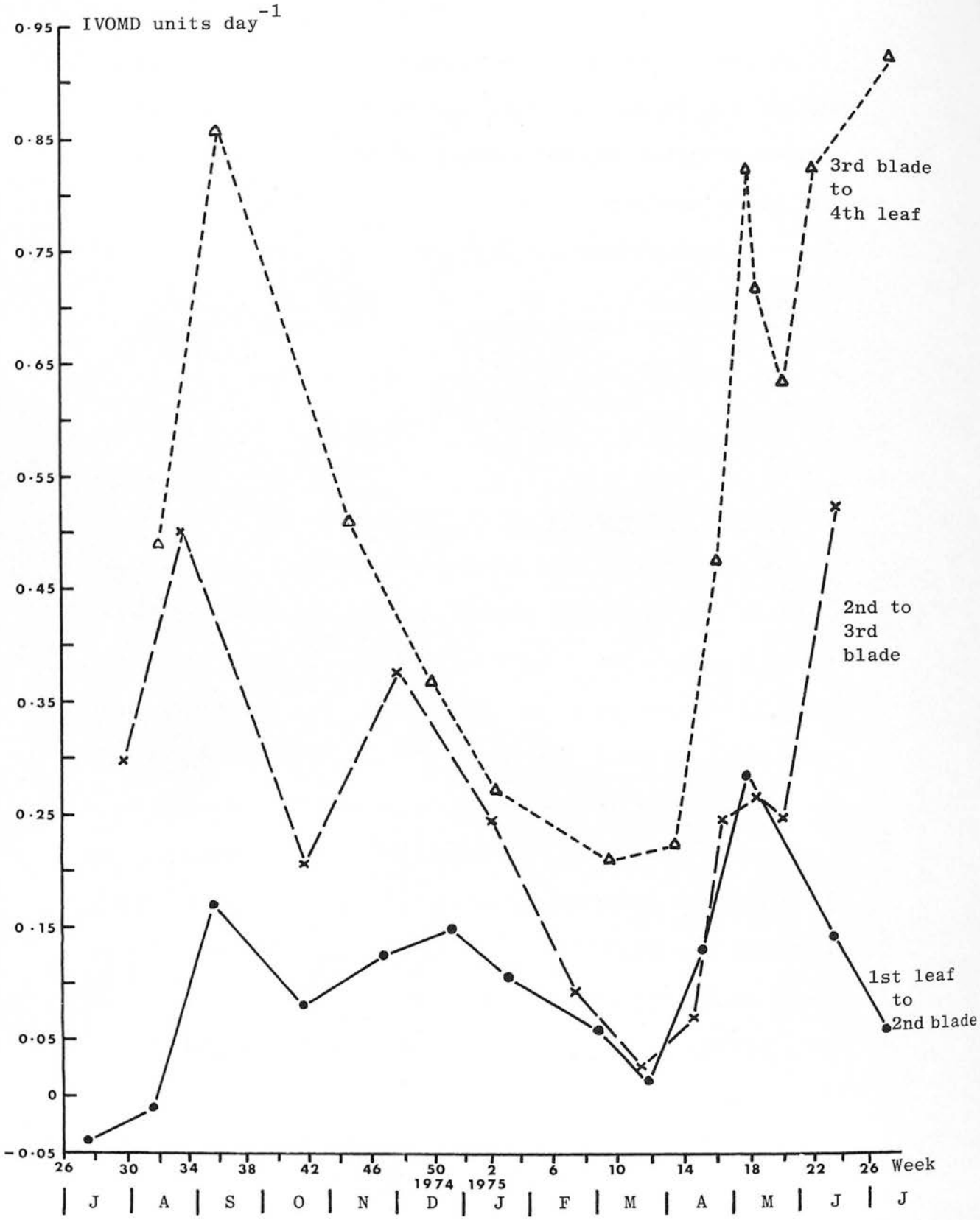


Fig. 4.3.17 : Rate of change in digestibility between
1st leaf and 2nd blade ●———●
2nd blade and 3rd blade ×— — -×
3rd blade and 4th leaf △- - - - -△, IVOMD units day^{-1}.
Positive rates of change represent a decline in digestibility from one leaf position to the next.

later (given by Fig. 4.3.4), the digestibility of the leaf blade was given by the mean digestibility of the 2B fraction at that time. One further leaf appearance interval later (again referring to Fig. 4.3.4), the digestibility of the blade was given by the digestibility of the 3B fraction on that day. The process was repeated to obtain the digestibility of the leaf once it had reached the 4th leaf position. It had to be assumed that a reasonable approximation to the digestibility of the 4th blade was given by the 4th leaf (blade + sheath). Separate measurements on 4th blade and 4th sheath on 4th June 1975 indicate that the approximation was reasonable at that time (IVOMD of 4th blade = 72% ± 1.2, IVOMD of 4th sheath = 73% ± 0.1).

Fig. 4.3.16 shows that leaves appearing in the autumn months lived longer, and declined to a lower level of digestibility by the time they were in the fourth leaf position on a tiller, than leaves appearing in the early summer months.

Rates of change in digestibility (Fig. 4.3.17)

The rates at which digestibility changes took place as leaves passed from one leaf position to the next were calculated.

Rate of change in digestibility between two successive leaf positions LP_A and LP_B, of mean digestibilities DIG_i and DIG_j on days DAY_i and DAY_j respectively, was given by:

$$\frac{DIG_j - DIG_i}{DAY_j - DAY_i}$$

and is represented in Fig. 4.3.17 as occurring on $\frac{DAY_i + DAY_j}{2}$, i.e. half way through the time it took for the leaf to age from leaf position LP_A to leaf position LP_B.

Changes in the rate of fall in digestibility from the 1st leaf to the 2nd blade followed, to some extent, changes in the leaf appearance interval (see Fig. 4.3.4). In contrast, the pattern of change in the rate at which digestibility fell between 3rd blade and 4th leaf followed fairly closely the pattern of change shown by the leaf death interval throughout the year (see Fig. 4.3.5).

Thus the rate of change in digestibility between 1st leaf and 2nd blade increased during weeks 34 - 36, 47 - 52 and 13 - 18; the leaf appearance interval was becoming shorter during each of these periods. The association is not invariable, however, as the rate of change in digestibility between 1st leaf and 2nd blade slowed down during two other periods when the leaf appearance interval was becoming shorter (weeks 4 - 13 and 19 - 22).

Leaf death intervals were shortest in week 36 1974 (early September) and week 25, 1975 (latter half of June), both times at which the third leaf was declining most rapidly in digestibility at a rate of approximately 0.85 OMD units per day.

REPRODUCTIVE TILLERS

The digestibilities of the parts of a reproductive tiller are shown in Table 4.3.7, together with the mean ages of the leaves. Only one duplicated sample per sampling date was analysed for each tiller part on the last four sampling dates. There are thus no standard errors available for these values. Apart from the digestibilities measured on May 5th, therefore, the values obtained must be regarded as tentative estimates.

Table 4.3.7 : Organic Matter Digestibility and Age (in days, underlined) of parts of the reproductive tiller.

Plant part	Sampling Date									
	5.5.75 OMD mean	5.5.75 OMD SE	5.5.75 age	21.5.75 OMD	21.5.75 age	26.5.75 OMD	26.5.75 age	3.6.75 OMD	3.6.75 age	3.7.75 OMD	3.7.75 age
1B	90.1 ± *0.61*		8.5	81.4	21	83.5	27	87.0	33	74.3	61
1S				70.4		70.3		72.4		58.8	
2B	87.6 ± *0.82*		16	80.0	29	81.3	35	83.8	42	61.7	69
2S	90.2 ± *0.27*			63.9		63.7		68.8		52.1	
3B	85.8 ± *0.28*		36	69.2	46	74.7	51	74.9	58	59.7	86
3S	83.4 ± *0.88*			-		62.3		64.2		53.4	
4B	83.5 ± *0.50*		71	63.2	77	62.7	82	61.1	88		
4S	83.4 ± *1.59*			-		-		-			
5B	77.8 ± *1.61*										
5S	72.3										
6L	62.6										
FLOWER				86.8		86.0		83.3		63.8	
STEM	89.5 ± *0.48*			75.0		72.5		73.1		52.0	

Since 80% of the flag leaves had emerged by May 5th (see section 4.3.2.8), the digestibility values obtained on each sampling date for a particular leaf position are those of the same leaf growing older.

On 5th May leaves 1 to 5 were alive (see section 4.3.2.11), where alive means less than 100% brown. On 21st May about 40%, on 26th May about 60%, and on 3rd June 80% of 4th leaves were dead.

By June 24th all the 3rd leaves had died so it is likely that by July 3rd many of the 2nd leaves would also have been dead.

It would appear that the digestibility of a blade remained in the 80's whilst it and the leaf below were probably still completely green. The digestibility of the blade then appears to have fallen to about 75% when the blade of the leaf below began to turn completely brown. 100% brown leaves had a digestibility of about 62%.

4.3.3.2 DRY WEIGHTS OF PLANT PARTS

VEGETATIVE TILLERS

Weights of each part of the tiller were determined on the dates and treatments listed on p. 135, except on November 6th and December 17th 1974. In December the relative weights of the separated fractions were determined but not the weights of the individual units.

(a) Seasonal changes in weights of leaf blades and sheaths

The dry weights of different parts of the tiller, of whole tiller (excluding litter), of the loose litter (expressed on a per tiller basis), and of a whole tiller plus its quota of loose litter, are tabulated in Appendix 6 for each nitrogen treatment throughout the year. Weights given in the table refer only to separated fractions in which most of the blades were intact and had not been damaged by a preceding cut.

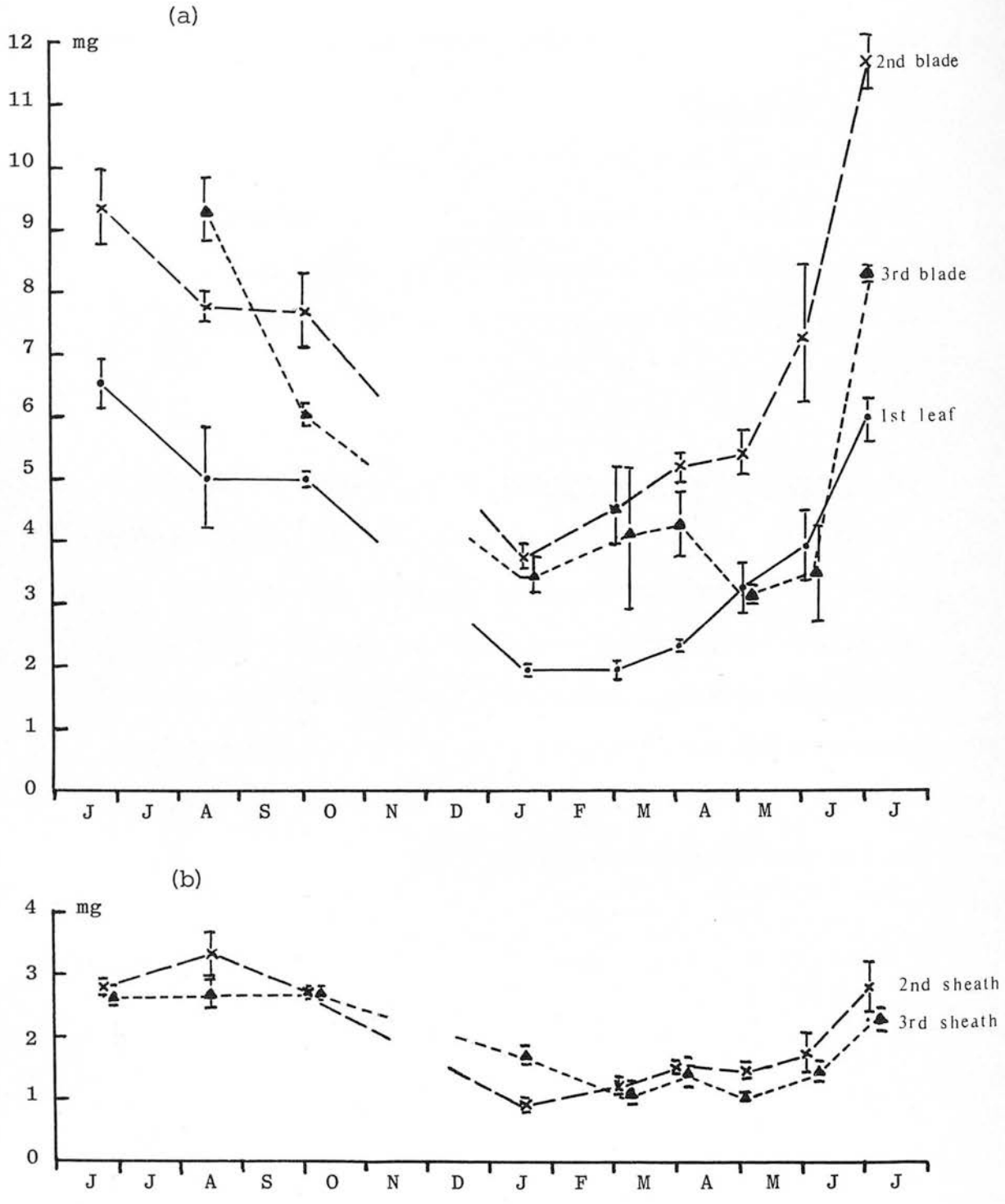


Fig. 4.3.18a : Weights of uncut 1st leaf (——), 2nd blade (— —) and 3rd blade (-----). Lowest nitrogen treatment (N1), mg.

Fig. 4.3.18b : Weights of 2nd sheath (— —) and 3rd sheath (-----). Treatment N1, mg.

Figures 4.3.18 a and 4.3.18 b show the weights of the 1st, 2nd and 3rd leaves (blades and sheaths separately) in the lowest (N1) nitrogen treatment at different times of the year. Weights in winter are about 1/3 of maximum weights in the summer, for all parts.

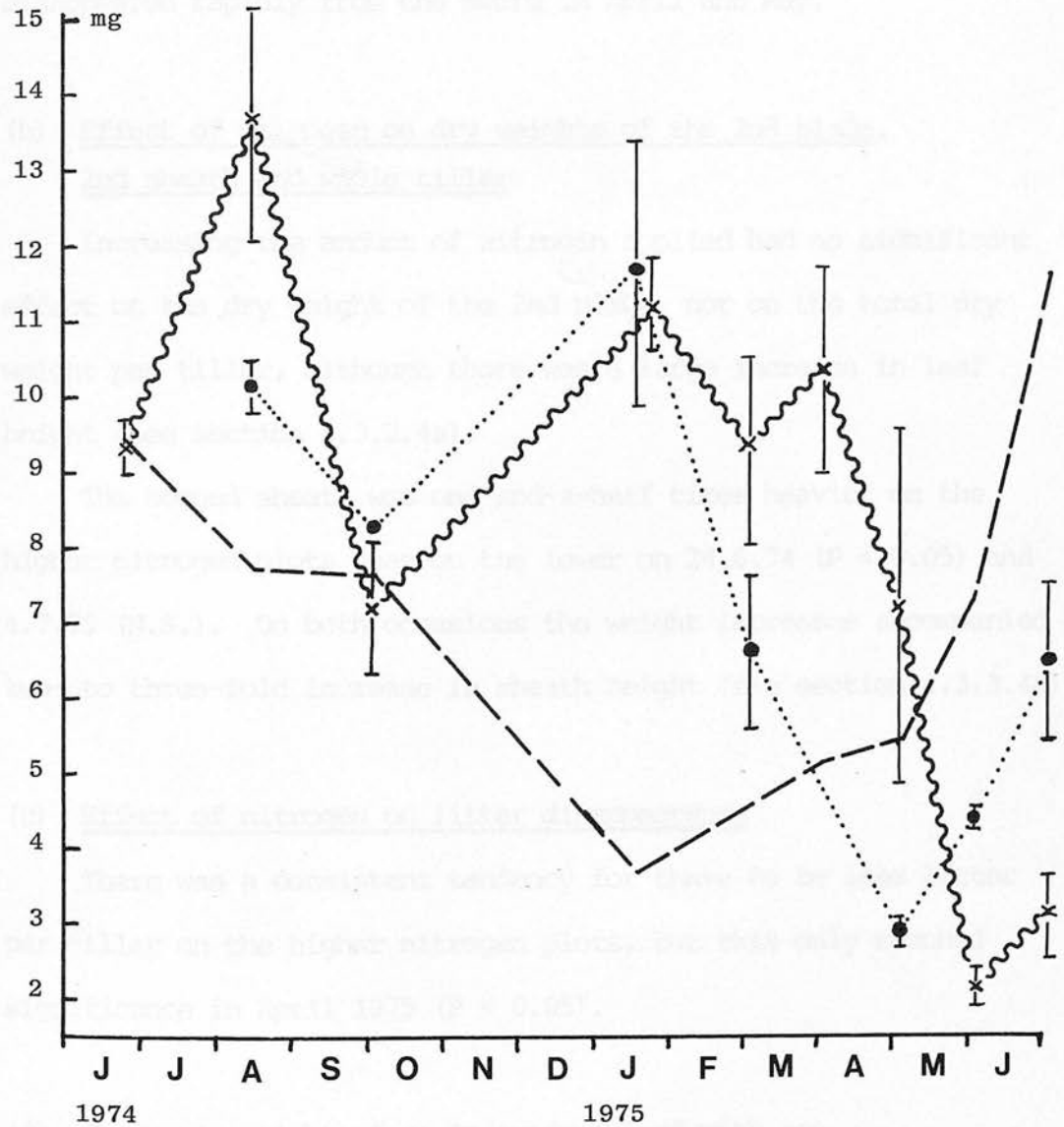


Fig. 4.3.18c : Dry weights of uncut 4th leaves (·····); and of loose litter (expressed as weight per tiller) (∿∿∿). The weight of the 2nd blade (— —) is given for comparison. Treatment N1. I = *S.E.*

The weights of the oldest material in the sward - the 4th leaf and the loose litter - are presented in Fig. 4.3.18c (treatment N1). The weight of the 2nd blade has been added for comparison. There was a build-up of litter per tiller in late summer which fell rapidly in September. After this it increased to a fairly steady net quantity over the winter. Litter disappeared rapidly from the sward in April and May.

(b) Effect of nitrogen on dry weights of the 2nd blade, 2nd sheath and whole tiller

Increasing the amount of nitrogen applied had no significant effect on the dry weight of the 2nd blade, nor on the total dry weight per tiller, although there was a large increase in leaf height (see section 4.3.3.4a).

The second sheath was one-and-a-half times heavier on the higher nitrogen plots than on the lower on 24.6.74 ($P < 0.05$) and 4.7.75 (N.S.). On both occasions the weight increases accompanied a two- to three-fold increase in sheath height (see section 4.3.3.4a).

(c) Effect of nitrogen on litter disappearance

There was a consistent tendency for there to be less litter per tiller on the higher nitrogen plots, but this only reached significance in April 1975 ($P < 0.05$).

(d) Change in weight of an individual leaf with age

Fig. 4.3.19 follows the change in weight of an individual leaf as it grows older. Weight changes were worked out for a new leaf every month. Information was used from the lowest nitrogen treatment (N1).

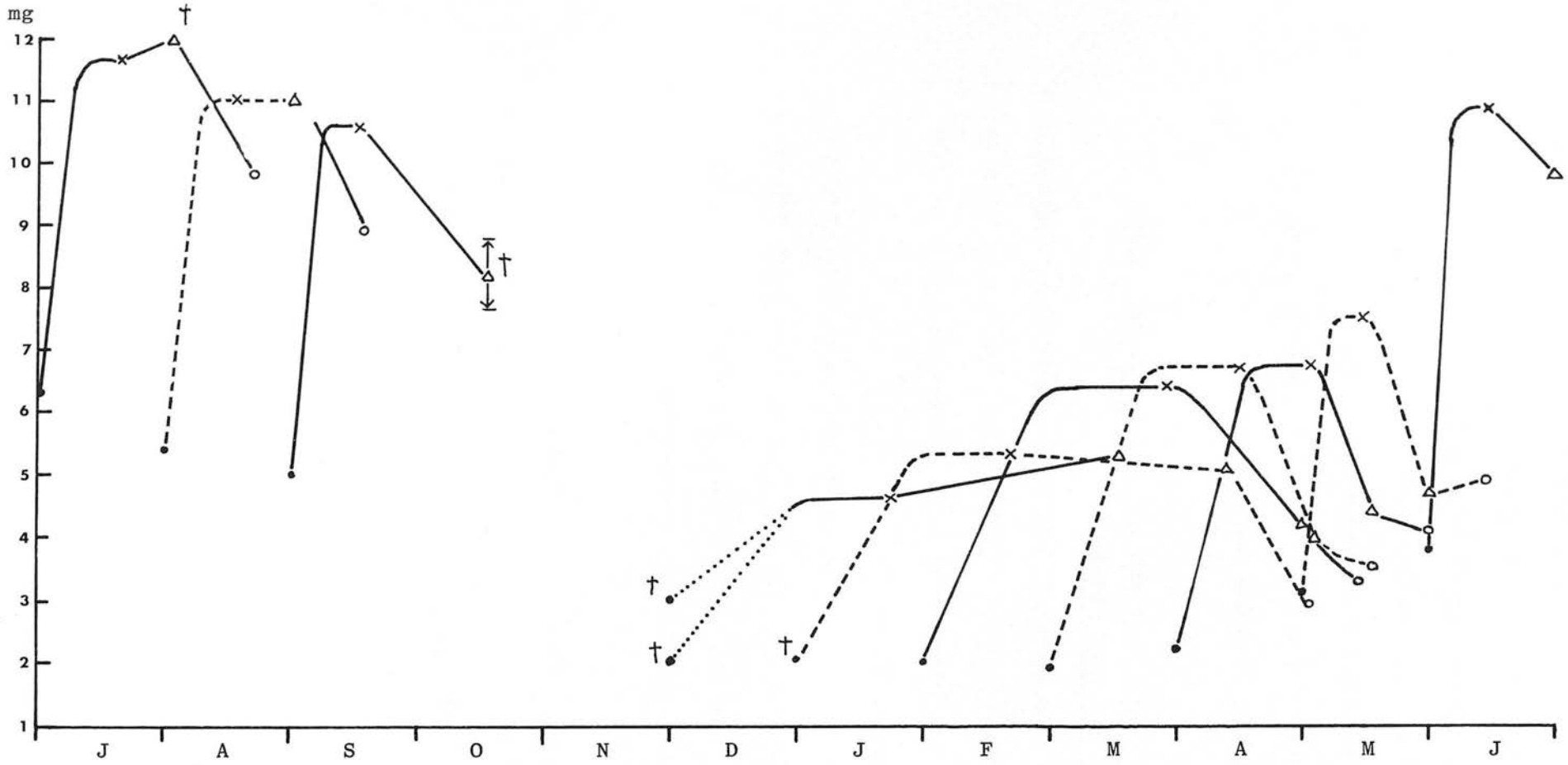


Fig. 4.3.19 : Change in weight of an individual leaf as it grows older. Nitrogen treatment N1.
Starting points (•) are half-emerged leaves on the first day of each month.

× = 1 leaf appearance interval later (2nd leaf weight = 2B + 2S).

△ = 1 further leaf appearance interval later (3rd leaf weight = 3B + 3S).

○ = 1 more leaf appearance interval later (4th leaf weight).

† = approximations from Fig. 4.3.18a.

Starting on the first day of the month the mean weight of the first leaf, obtained from Fig. 4.3.18a, is that of a leaf one half of a leaf appearance interval in age (see section 4.3.3.1c, p.140). This is based upon the assumption that leaves increase in weight linearly as they expand.

It was then assumed that the leaf reached its mature weight at approximately the time when it first became fully expanded (ligule appeared), i.e. ½ a leaf appearance interval later. It was further assumed that the mature weight would be approximately equal to the mean weight of the 2nd leaf (2B + 2S) given that visible signs of senescence (and possibly, therefore, accompanying weight loss) are not generally observed in the 2nd leaf position.

One leaf appearance interval later the weight of the leaf was taken to be equal to the mean weight of the 3rd leaf (3B + 3S). Similarly, after a further leaf appearance interval, weight was set equal to the mean weight of the 4th leaf at that time.

A doubling in leaf weight would be expected between half-emergence and full-emergence if leaves were expanding at a constant rate, and if weight increases linearly with leaf extension. Increases of about 100% were observed in July, August and September 1974. From February to June 1975, however, larger increases of 150 to 200% were observed. During these months it is likely that the later stages of a leaf's expansion take place under more favourable conditions than those existing during the earlier stages, since light and temperature conditions are improving. It may, therefore, be expected that leaves grew faster in the latter portion of their leaf appearance interval, leading to weight increases greater than 100%.

Weight was lost between the 2nd and 3rd leaf positions in April (34% to 40%), May (37%) and June (9%) 1975. Leaves appearing in early September also lost weight (about 20%) between these positions, whereas leaves appearing in middle or late September may have gained. (The very great change in leaf lifespan between mid-August and mid-September has already been referred to (Section 4.3.2.3)). At all other times there was either no weight loss, or a small gain.

Weight loss between the 3rd and 4th leaf positions was about 19% in August and September 1974, and 39% in late April 1975. At other times of the year there was little change from 3rd to 4th leaf.

The large weight losses in April and May, and the smaller losses in August and September, may have been associated with the development of reproductive tillers in the sward.

Rates of change in leaf weight

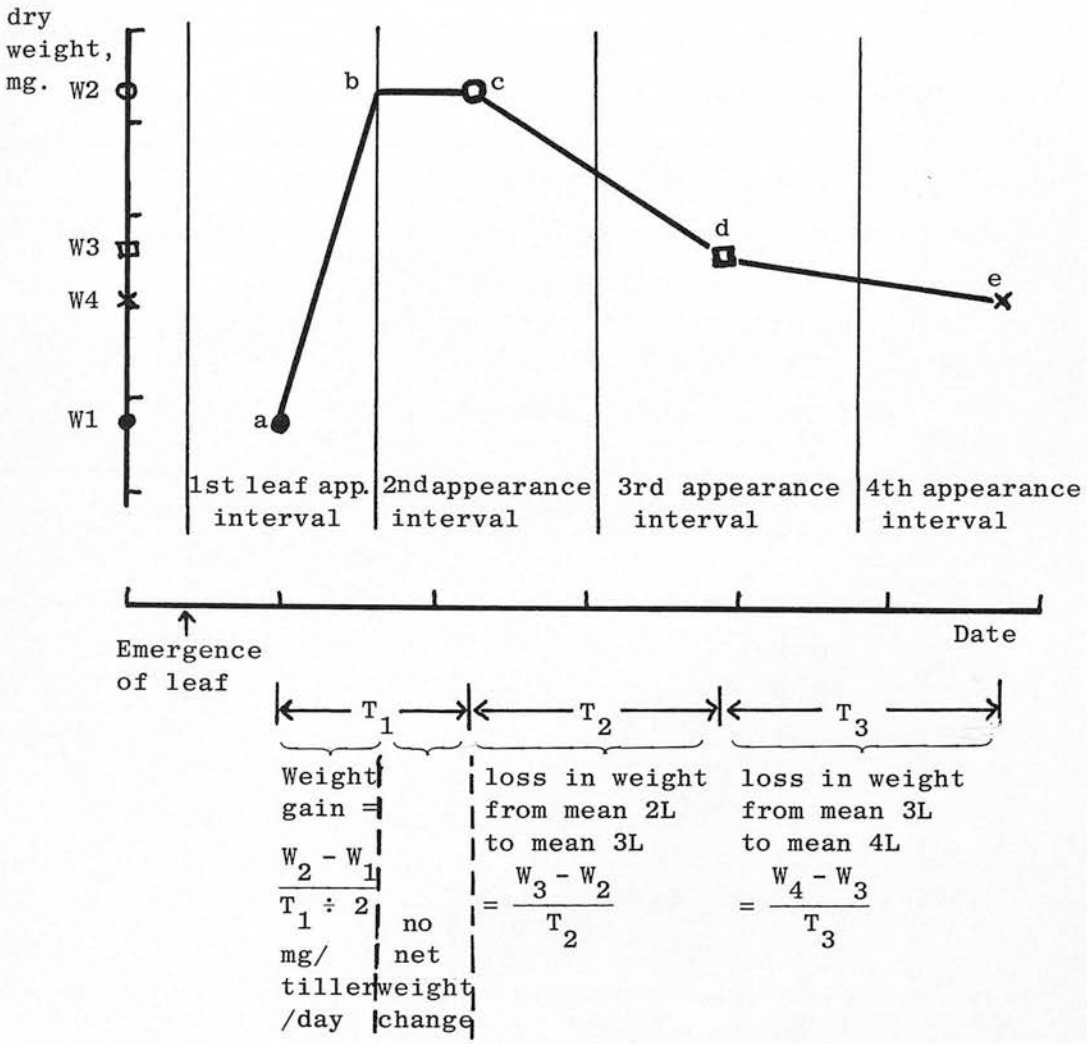
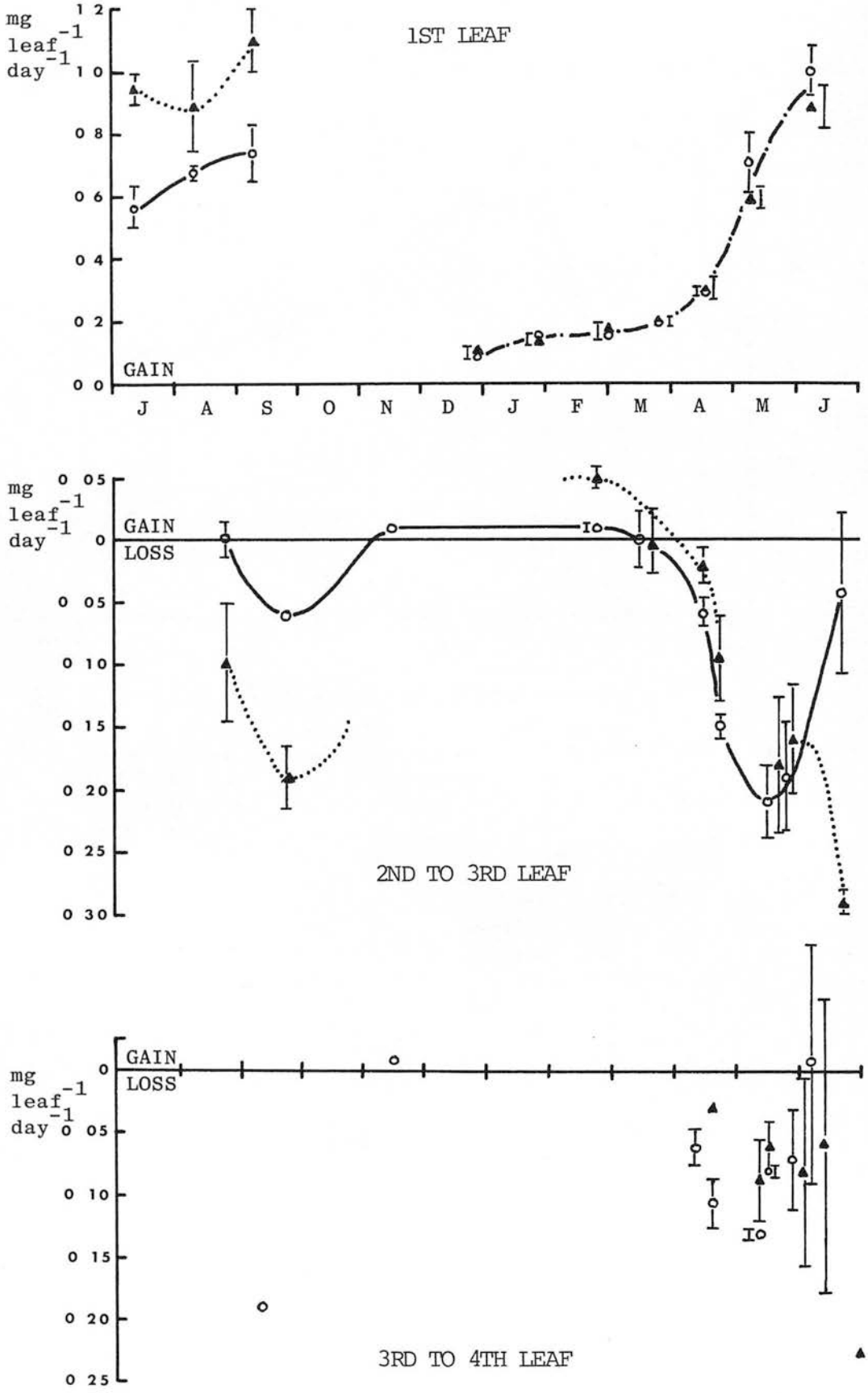


Fig. 4.3.20 : Model used to calculate rates of change in leaf weight, mg $tiller^{-1}$ day^{-1}.

Rates of change in leaf dry weight under lowest (N1) and highest (N4) nitrogen treatments are given in Table 4.3.8.

A discontinuous model of weight changes was adopted in calculating these rates in accordance with the assumptions already made in considering changes in leaf weight with age (p. 152).



Rates of gain and loss in weight at different leaf positions (from Table 4.3.8). N1 N4

Table 4.3.8 : Rates of change in dry weight of an individual leaf. mg leaf^{-1} day^{-1}. Vegetative tillers.

S.E. of 3 replicates given in italics.

* = 2 replicates only † = 1 replicate only

Date of leaf emergence	Rate of growth of 1st leaf (a to b in Fig. 4.3.20) mg leaf^{-1} day^{-1} N1	N4	Rate of wt. loss mid-2nd to mid-3rd leaf positions (c to d in Fig. 4.3.20) mg leaf^{-1} day^{-1} N1	N4	Rate of wt. loss mid-3rd to mid-4th leaf positions (d to e in Fig. 4.3.20) mg leaf^{-1} day^{-1} N1	N4
1. 7.74	JULY 1 - 20		JULY 18 - AUG 7		AUG 6 - 23	
	0.569	0.941				
	0.066	*0.052*				
1. 8.74	AUG 1 - 18		AUG 16 - SEPT 4		SEPT 1 - 17	
	0.682	0.889	0.000	0.097	0.188†	
	0.014	*0.144*	*0.014*	*0.050*		
1. 9.74	SEPT 1 - 18		SEPT 13 - OCT 6		OCT 3 - NOV 8	
	0.739	1.098	0.062	0.187		
	0.095	*0.105*		*0.027*		
1.12.74	DEC 1 - JAN 22		JAN 20 - MAR 29		MAR 14 - MAY 1	
	0.103	0.091	-0.008	-0.052	0.058*	
	0.011	*0.006*	*0.003*	*0.009*	*0.015*	
1. 1.75	JAN 1 - FEB 21		FEB 9 - APR 22		MAR 29 - MAY 10	
	0.136	0.152	0.000	0.004	0.105	0.033†
	0.026	*0.003*	*0.023*	*0.022*	*0.018*	
1. 2.75	FEB 1 - MAR 28		MAR 21 - MAY 10		APR 24 - MAY 28	
	0.167	0.155	0.058	0.022	0.132*	0.086
	0.012	*0.014*	*0.008*	*0.013*	*0.004*	*0.035*
1. 3.75	MAR 1 - APR 18		APR 11 - MAY 8		MAY 2 - 26	
	0.195	0.199	0.150	0.094	0.079*	0.058
	0.009	*0.028*	*0.016*	*0.035*	*0.004*	*0.019*
1. 4.75	APR 1 - MAY 4		APR 29 - MAY 30		MAY 10 - JUNE 11	
	0.289	0.300	0.209	0.177	0.070*	0.083
	0.018	*0.044*	*0.032*	*0.057*	*0.041*	*0.072*
1. 5.75	MAY 1 - 15		MAY 13 - JUNE 4		MAY 27 - JUNE 16	
	0.707	0.593	0.187	0.161	-0.008*	0.057
	0.096	*0.033*	*0.044*	*0.044*	*0.096*	*0.120*
1. 6.75	JUNE 1 - 15		JUNE 10 - JULY 4		JUNE 19 - JULY 7	
	0.997	0.876	0.043	0.290*		0.224
	0.082	*0.080*	*0.064*	*0.007*		*0.031*

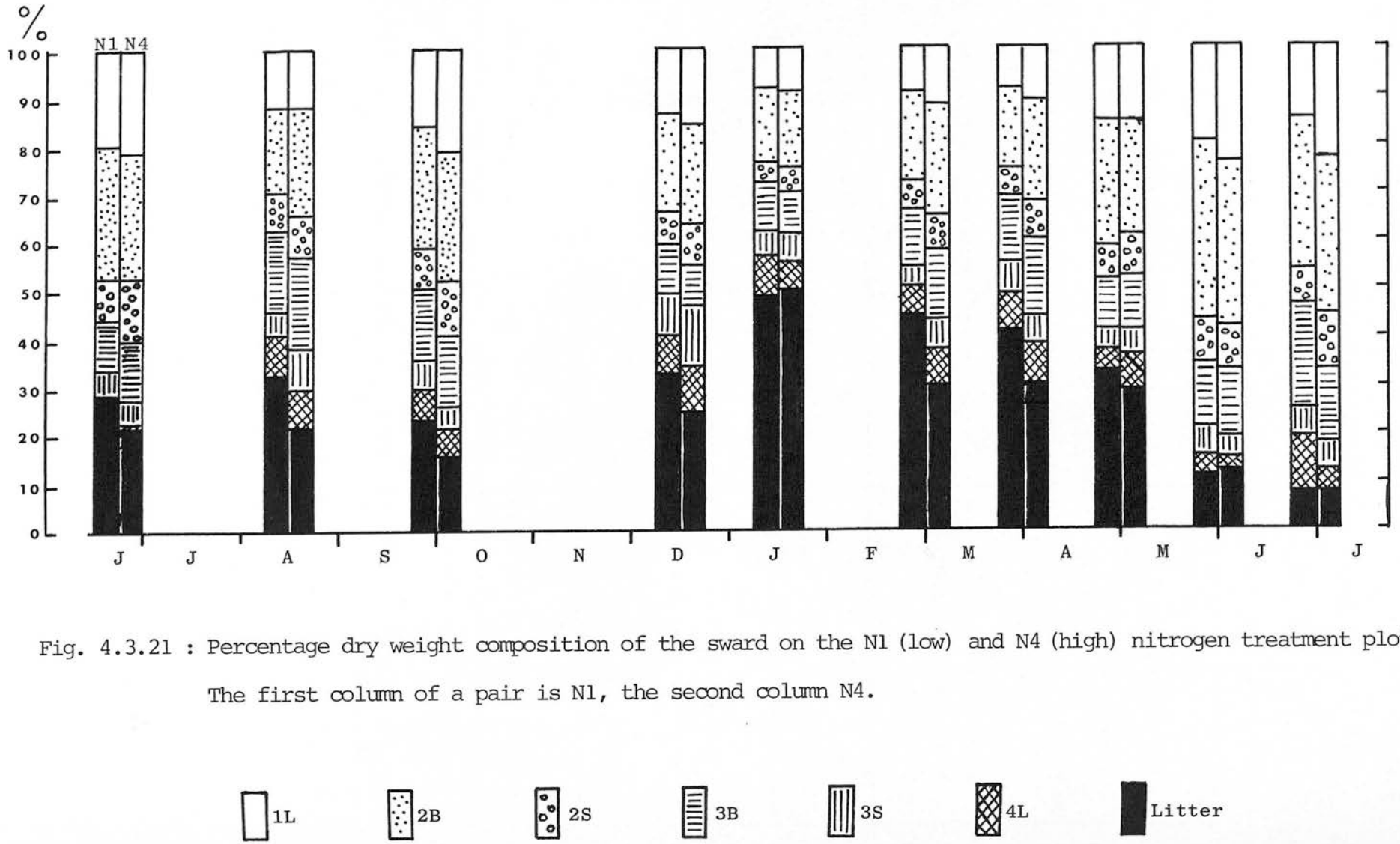


Fig. 4.3.21 : Percentage dry weight composition of the sward on the N1 (low) and N4 (high) nitrogen treatment plots. The first column of a pair is N1, the second column N4.

(e) Distribution of weight between blade and sheath

The weight changes calculated refer to whole leaves. From the weights given in Appendix 6, the ratios of $\frac{2S}{(2B+2S)}$ and 3S/(3B+3S) were calculated.

Ratio of 2nd sheath to 2nd (blade + sheath)

	24.6	14.8	2.10	17.1	4.3	4.4	4.5	4.6	4.7
N1	23	30	26	20	20	23	21	19	19
N2	22	29	27					20	27
N3	32	28	27						
N4	34	28	29	24	22	26	24	20	25

Mean ratio over all N levels = 25%

Ratio of 3rd sheath to 3rd (blade + sheath)

	24.6	14.8	2.10	4.3	4.4	4.5	4.6	4.7
N1		23	31	20	26	25	29	21
N2		25	32				27	26
N3		28	27					
N4		29	27	20	23	31	24	27

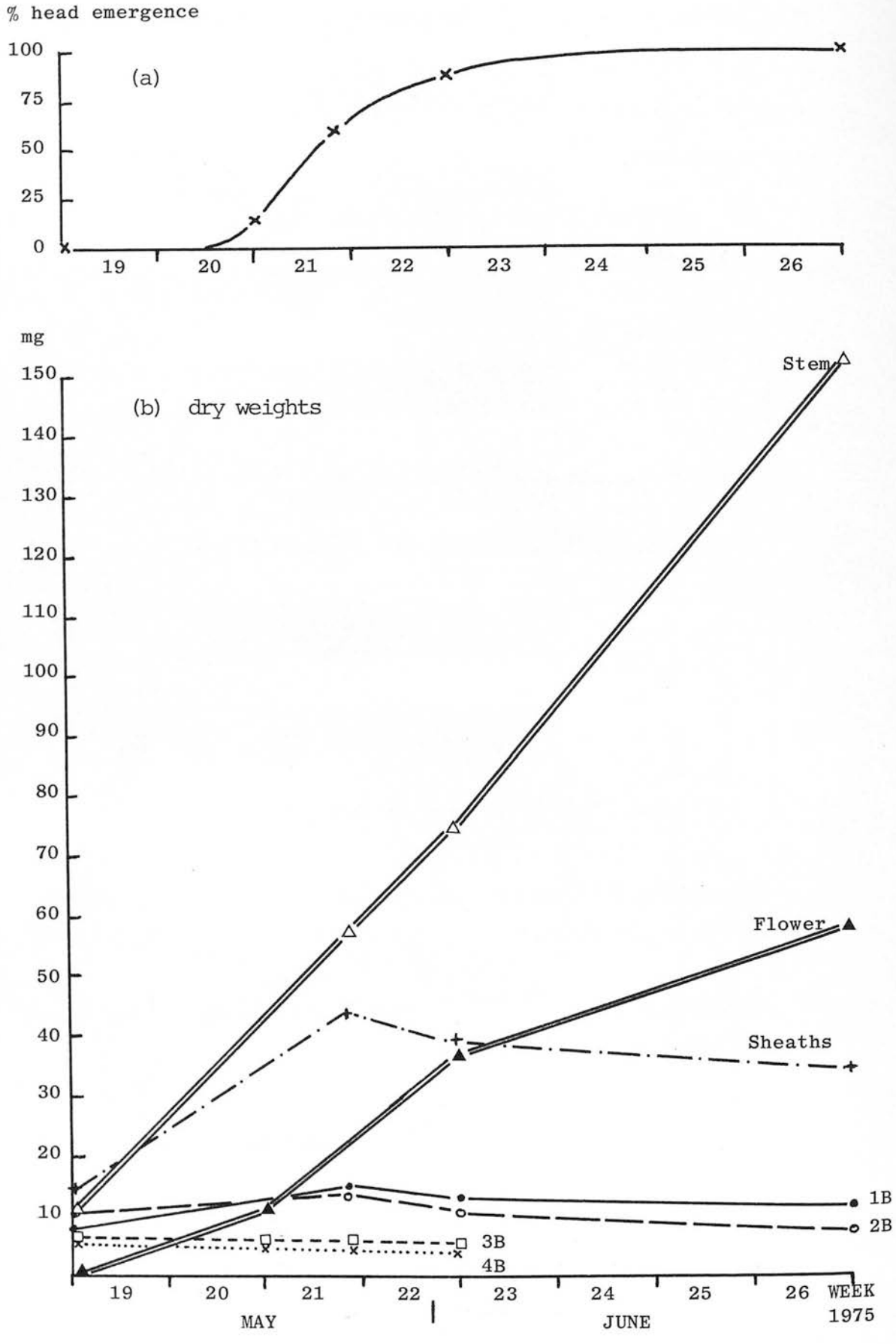
Mean ratio over all N levels = 26%

The ratios for December (2L and 3L) and January (3L) cannot be calculated since there were too many cut leaves in the samples.

(f) Composition of the sward in terms of the relative dry weights of the different parts

The % dry weight of the sward contributed by each of the constituent parts is represented in Fig. 4.3.21 for the lowest and the highest nitrogen treatments.

The two youngest leaves (1L + 2B + 2S) made up 40 - 60% of the sward by dry weight between early May and early October, and 30 - 40% over the winter months. Dead and 4th leaf material made up 40 - 55% of the sward in winter and 15 - 25% in June and July.


% head emergence
100
75
50
25
0
(a)
19
20
21
22
23
24
25
26
mg
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
(b) dry weights
Stem
Flower
Sheaths
1B
2B
3B
4B
19
20
21
22
23
24
25
26
WEEK
1975
MAY
JUNE

REPRODUCTIVE TILLERS

(g) Weights of stem, flower, blades and sheaths

The dry weights of the individual parts of a reproductive tiller are shown in Fig. 4.3.22b. The tillers were growing in uncut, primary growth swards which had been fertilized with 125 Kg ha^{-1} of 29-5-5 compound fertilizer on 17.4.75.

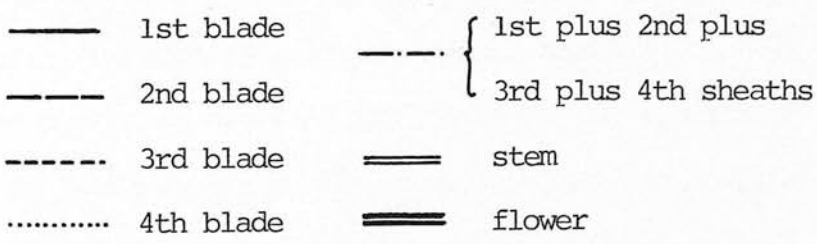
The percentage head emergence, determined from the same samples, is shown in Fig. 4.3.22a. A similar rate of head emergence was also measured in the permanently-labelled tillers used for leaf appearance and death records.

The stem increased in weight by an average of 2.518 mg $tiller^{-1}$ day^{-1} between May 6th and July 1st 1975. The flowering head grew by an average of 0.752 mg $tiller^{-1}$ day^{-1} from May 6th to 21st, and June 3rd to July 1st. Between May 21st and June 3rd - the period during which ears were emerging - the flowering head increased in growth rate to 1.975 mg $tiller^{-1}$ day^{-1}.

From May 6th to May 26th an increase in weight also occurred in the first leaf (blade + sheath) of 1.369 mg day^{-1}. The rate of increase in weight of the 1st leaf was thus twice as fast in reproductive tillers as in vegetative tillers during the same period (see p.155).

Fig. 4.3.22a : % head emergence during primary growth.

Fig. 4.3.22b : Changes in dry weight (mg) of parts of the reproductive tiller during primary growth.



The 2nd, 3rd and 4th sheaths were similar in weight to the corresponding blades. The 1st sheath is 8 mg heavier than the 1st blade from the end of week 21 onwards.

Adding together the three sites of weight increase gives an estimate of the rate of new growth per reproductive tiller per day:

Weight of new growth, mg (reproductive tiller)$^{-1}$ day^{-1}

	6.-21.5.75	21.-26.5.75	26.5.-3.6.75	3.6.-1.7.75
1st (flag) leaf	1.369	1.369		
Stem	2.158	2.158	2.158	2.158
Flower head	0.752	1.975	1.975	0.752
Total	4.279	5.502	4.133	2.190

Weight loss per tiller can also be estimated. The net change in weight of the 2nd plus older leaves from May 6th - 26th was +0.300 mg tiller^{-1} day^{-1}. (2B = +0.130, 2S = +0.336, 3B = -0.023, 3S = +0.036, 4B = -0.053, 4S = -0.039, 5L = -0.062 and 6L = -0.025). Between May 26th and June 3rd a total of 1.712 mg tiller^{-1} day^{-1} was lost from the leaf blades and sheaths. (1B = -0.276, 1S = -0.157, 2B = -0.359, 2S = -0.175, 3B = -0.149, 3S = -0.281, 4B = -0.127, 4S = -0.048, 5L = -0.084, 6L = -0.056).
From 3rd June to 1st July the loss was 0.426 mg tiller^{-1} day^{-1}. (1B = -0.048, 1S = -0.047, 2B = -0.101, 2S = -0.080, 3B = -0.047, 3S = +0.003, 4B = -0.102, 4S = -0.049, 5L = -0.041).

The net increase in weight per reproductive tiller is calculated from the balance of weight gain against weight loss:

Net increase in weight (mg reproductive tiller^{-1} day^{-1})

6.-21.5.75	21.-26.5.75	26.5.-3.6.75	3.6.-1.7.75
4.579	5.802	2.421	1.764

4.3.3.3 VERTICAL DISTRIBUTION OF BLADE AND SHEATH IN THE SWARD

VEGETATIVE TILLERS

(a) Heights of blade and sheath in the sward

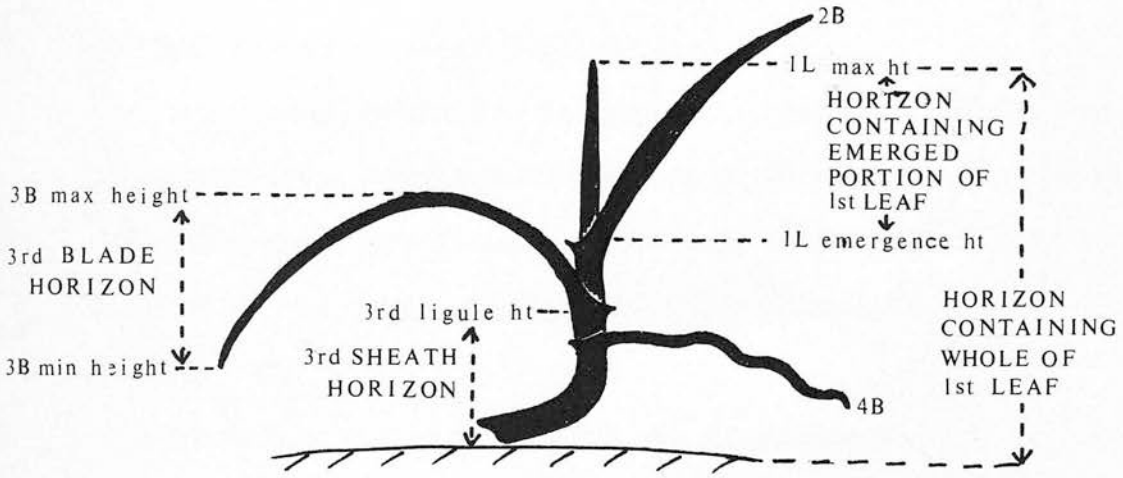


Fig. 4.3.23 : Diagram illustrating the height measurements made. Note that minimum height normally equals ligule height except when the leaf bends right over, as shown by leaf 3 in this diagram.

The heights above ground level of the highest and lowest points on a leaf blade, and the height of the ligule, were measured at each leaf position on the dates and treatments listed on page 135, apart from November 6th and December 17th 1974. The results are tabulated in Appendix 7 and refer to entire leaves only. Each measurement was made on approximately 54 tillers, but cut leaves were excluded from calculations of the means.

The height measurements describe the vertical distribution of material within the sward by giving the upper and lower boundaries

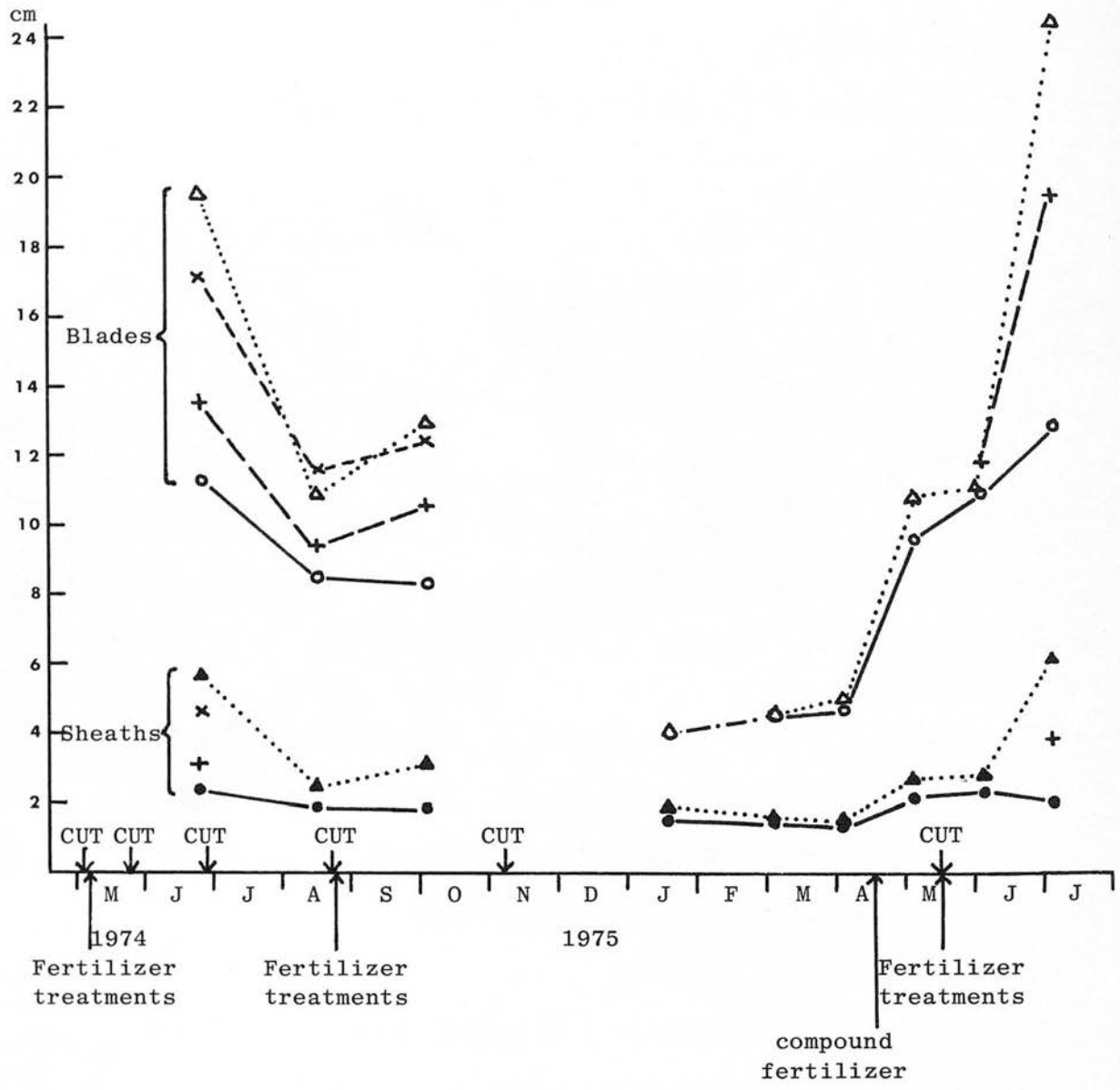


Fig. 4.3.24 : Effect of nitrogen fertilizer and time of year on the maximum heights of the 2nd blade (open symbols) and 2nd sheath, i.e. ligule height, (blocked symbols).

o——o N1 0 Kg N ha^{-1} in May; 23 Kg N ha^{-1} in August

+— —+ N2 67 " " " " ; 45 " " " "

×- - -× N3 134 " " " " ; 67 " " " "

Δ·····Δ N4 202 " " " " ; 90 " " " "

of the strata within which the leaf blades (1L, 2B, 3B, 4B) and sheaths occurred.

The maximum heights of the first fully emerged blade (2B) and its sheath are shown in Fig. 4.3.24 for each nitrogen treatment. The actual heights are specific to the particular year, soil and sward management applied.

The maximum height of the 2nd blade changed enormously with season and after sward management cuts or fertilization. Over the winter the height remained relatively constant at 4 to 5 cm, the same as the height to which the plots had been cut on November 7th.

The height of the sheath did not change much during the year under the low nitrogen treatment (N1); there was no elongation in May as in reproductive tillers.

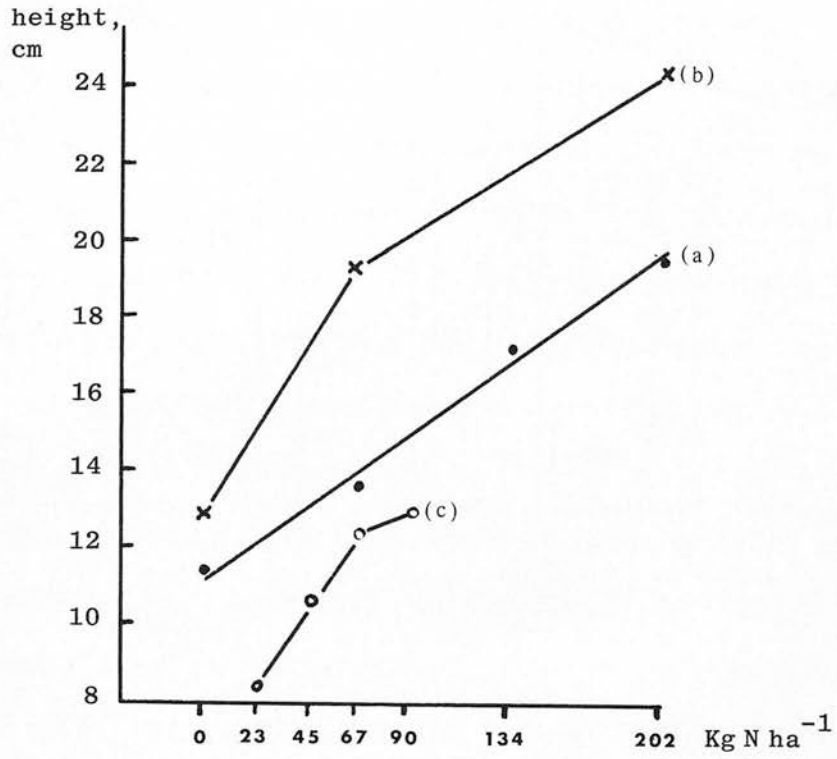


Fig. 4.3.25 : Effect of nitrogen fertilizer on the maximum height of the 2nd blade.

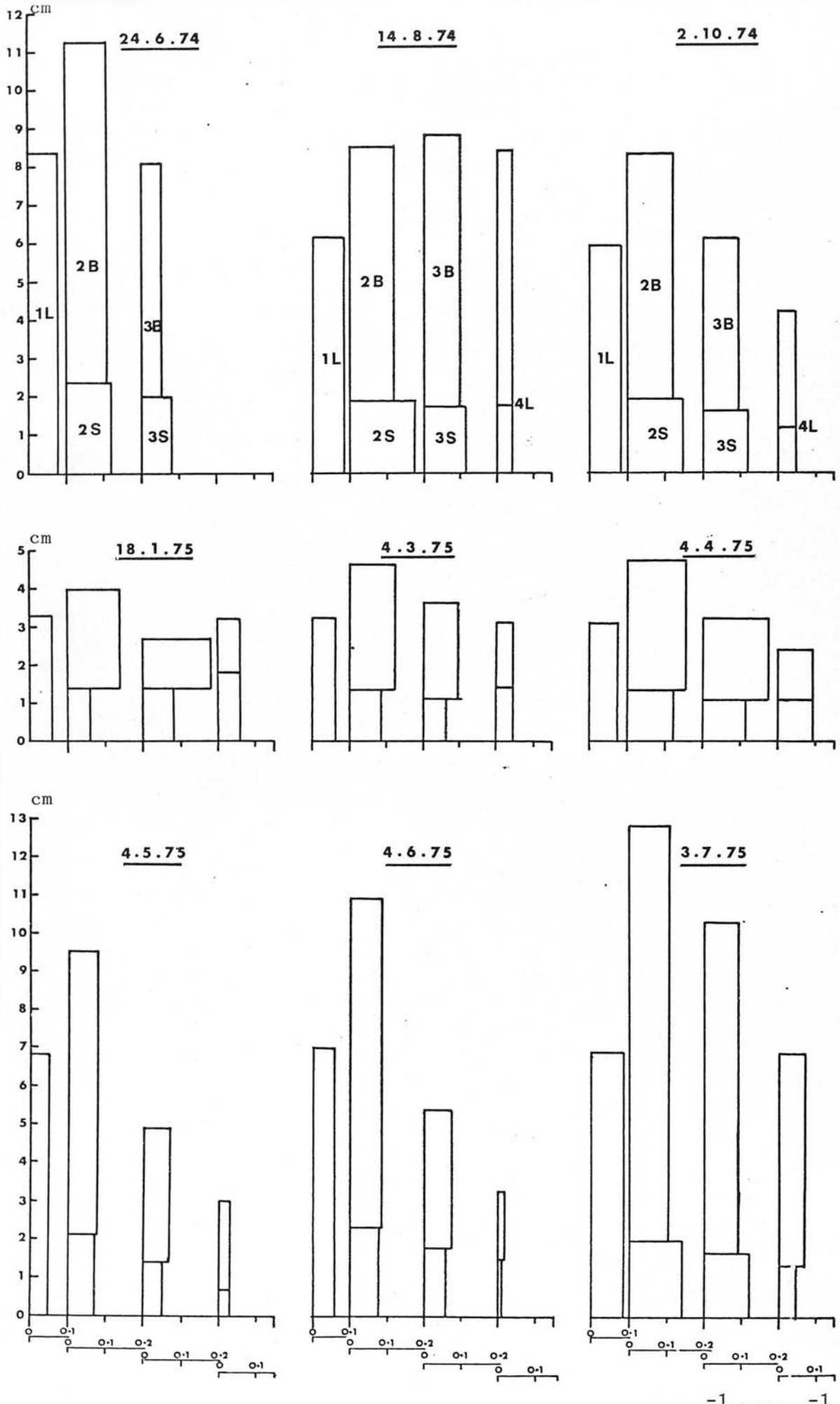
(a) 49 days after fertilizer application on 6.5.74

(b) 49 " " " " " 16.5.75

(c) 40 " " " " " 23.8.74

The response to the level of nitrogen applied was greatest between 0 and 67 Kg N ha^{-1} after the August 1974 (0.09 cm Kg^{-1} N) and May 1975 (0.10 cm Kg^{-1} N) applications. Above 67 Kg N^{-1} ha^{-1} the responses in August 1974 and May 1975 fell to 0.02 and 0.04 cm Kg^{-1}N respectively. A lower response per Kg N applied was obtained from the May 1974 fertilizer treatments (0.04 cm Kg^{-1} N ha^{-1}).

Sheath height was 2½ to 3 times greater in treatment N4 relative to treatment N1 7 weeks after both the May 1974 and May 1975 applications.


cm
24.6.74
14.8.74
2.10.74
1L
2B
3B
4L
2S
3S
cm
18.1.75
4.3.75
4.4.75
cm
4.5.75
4.6.75
3.7.75
0·1
0·2
mg cm^{-1} tiller^{-1}

(b) Dry weights of plant parts in different horizons

The distributions by weight and height of the youngest to oldest leaves in a sward are illustrated in Fig. 4.3.26. The values were obtained from vegetative tillers growing under the lowest nitrogen treatment (N1). The y-axis shows the boundaries of the horizon within which a particular plant part (e.g. 2B) lay. The x-axis represents the mean dry weight per unit height of that plant part in the sward.

Mean dry weight per unit height of blade material and of sheath material at each leaf position (1, 2, 3, 4 and 5) was calculated on a per tiller basis, not a per leaf basis. In other words, if W = wt. of 3rd blade, N = no. of tillers separated, and P = no. of tillers with the third blade present, then the mean weight a plant fraction per unit height in the sward = $\frac{W}{N}$ and not $\frac{W}{P}$. The area of a block (x × y) therefore equals the mean weight of leaf at that position per tiller.

In January, March and early April, leaves of all ages occupied similar horizons. In May and June the 2nd blade stood out above the younger and older material but by July and August the 3rd blades occupied almost as great a depth as the 2nd blades.

Fig. 4.3.26 : Vertical distribution of dry matter in the sward under the lowest (N1) nitrogen treatment, at different times of the year.

1L = 1st leaf

2L = 2nd blade (upper block) + 2nd sheath (lower block)

3L = 3rd blade " " + 3rd " " "

4L = 4th leaf

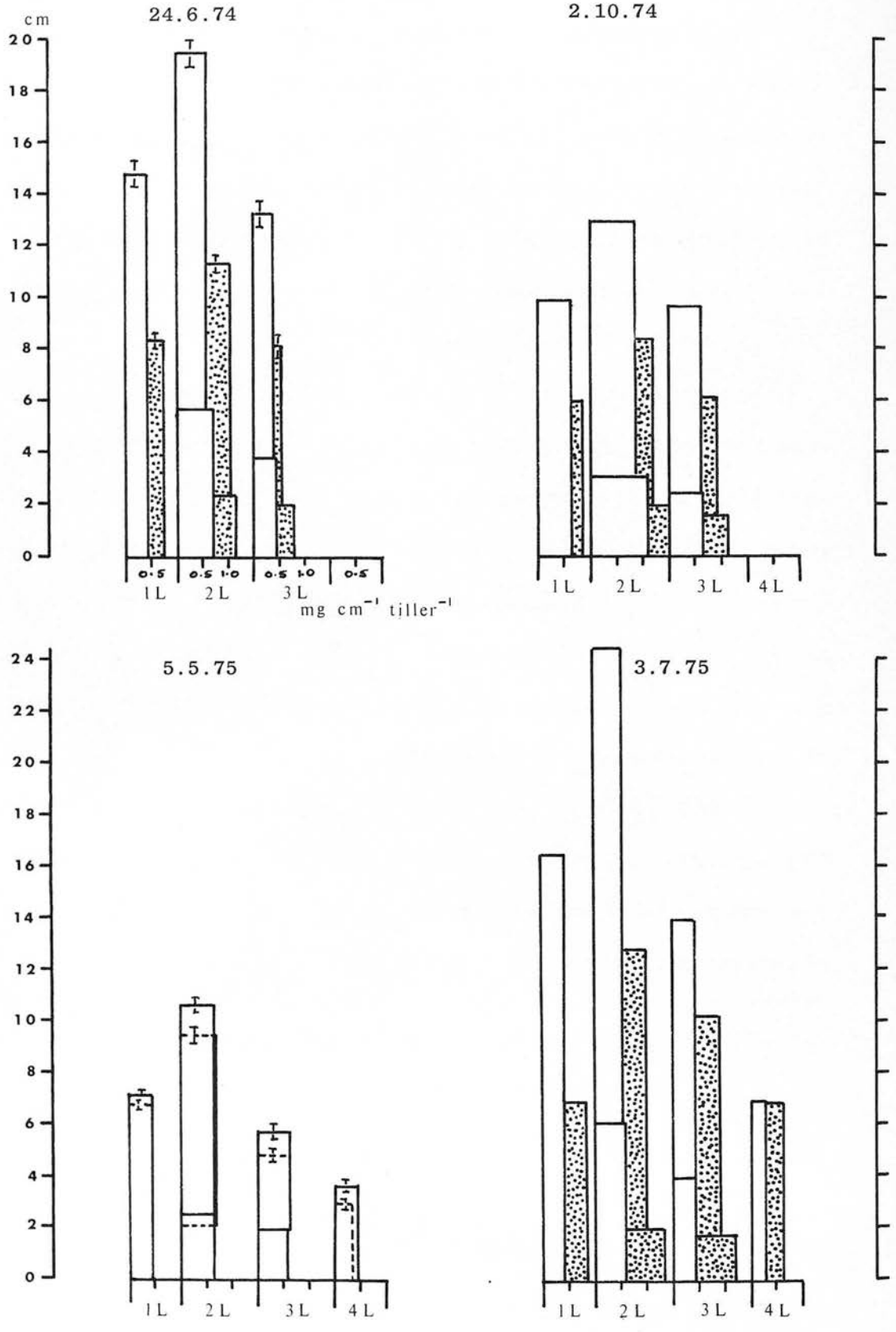

cm
24.6.74
2.10.74
0
2
4
6
8
10
12
14
16
18
20
0·5
0·5 1·0
0·5 1·0
0·5
1 L
2 L
3 L
4 L
mg cm⁻¹ tiller⁻¹
5.5.75
3.7.75
0
2
4
6
8
10
12
14
16
18
20
22
24

Fig. 4.3.27

Nitrogen fertilizer

The effect of applied nitrogen on the distribution of dry matter within the sward is illustrated in Fig. 4.3.27.

Although nitrogen had very little effect on leaf weight (see section 4.3.3.3b), it did have a very big effect on leaf length and therefore on the vertical distribution of dry matter. There was a corresponding decrease in leaf weight per unit height at higher levels of nitrogen fertilizer.

On May 5th 1975 the evidence shows very little residual effect of the 1974 fertilizer treatments on the vertical distribution of dry matter in the sward.

Fig. 4.3.27 : Vertical distribution of dry matter in the sward under the lowest (N1) and highest (N4) nitrogen treatments.
Shaded blocks represent N1; superimposed on shaded blocks are the unshaded blocks of treatment N4.
1L = 1st leaf
2L = 2nd blade (upper block) + 2nd sheath (lower block)
3L = 3rd blade (" ") + 3rd " (" ")
4L = 4th leaf
S.E.'s are shown by I.

y axis = height, cm
x axis = weight per unit height, mg cm^{-1} $tiller^{-1}$.

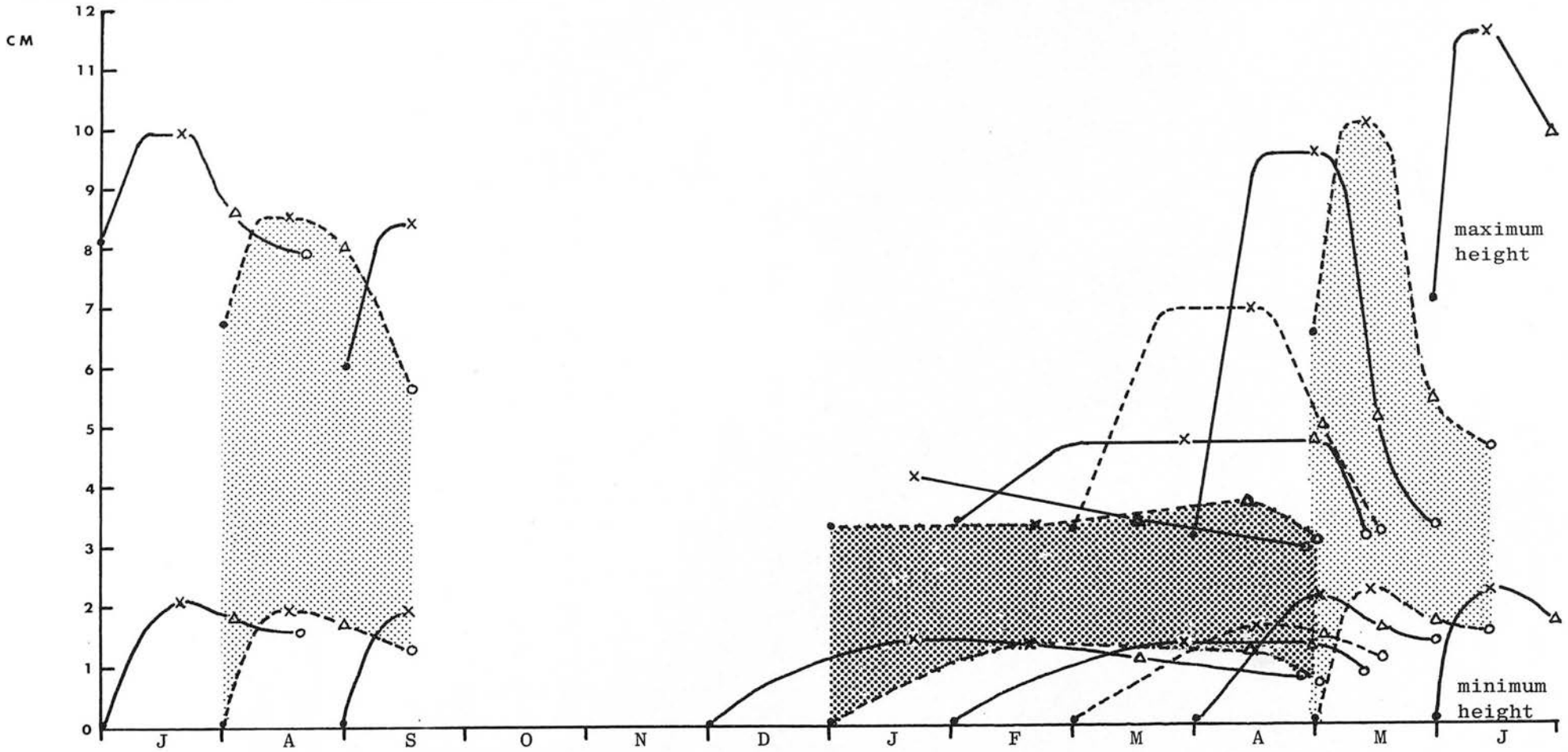


Fig. 4.3.28 : Change in the horizon occupied by a leaf as it ages. Treatment N1, vegetative tillers.

• height of a half-emerged leaf; × height in 2nd leaf position

△ height in 3rd leaf position; ○ height in 4th leaf position

The horizons occupied by blades half-emerged on August 1st 1974, January 1st and May 1st 1975, have been shaded for clarity.

(c) Changes in the horizon occupied by a leaf as it ages

Fig. 4.3.28 shows the upper (maximum) and lower (minimum) heights of leaf blades as they grew older.

On the first day of a particular month, the highest point on a half-emerged leaf is the mean height of the first leaf. The lowest point occurs at the height of the apex which is assumed to be at ground level in the vegetative tiller; it is recognised that this is not necessarily the case but in the material dealt with it is a reasonable approximation.

It was then assumed that the leaf reached its maximum height when leaf extension was complete, i.e. one leaf appearance interval after the leaf's emergence. Maximum height was taken to be equal to the mean upper (maximum) height of the 2nd leaf; this is likely to be an underestimation, except in short swards, as leaves have probably bent over by the time they are half-way through the second leaf appearance interval.

2½ leaf appearance intervals after emergence the highest point on the blade equals the average maximum height of the 3rd blade. One leaf appearance interval later the highest point is the average maximum height of the 4th blade.

Sheath heights (ligule height) were plotted in the same way.

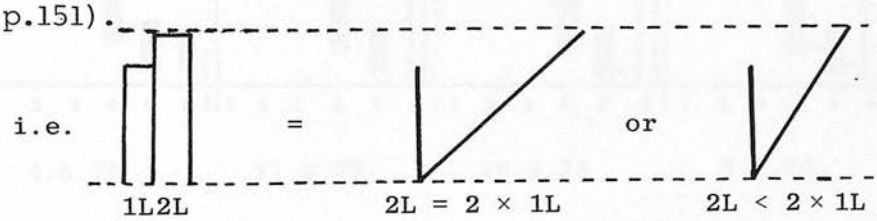
The upper boundary of the blade's horizon varied considerably with leaf age and with season of the year, particularly during March - June 1975. The lower boundary showed little change.

The horizon occupied by a leaf depends partly on its length and partly on how much it bends over. By referring to Fig. 4.3.26 it can be seen that leaves which appeared in December, January and

February must have bent over a lot, perhaps by as much as 60° (cosine of ½), between the 1st and 2nd leaf positions: a half-emerged leaf would have grown to twice its length by the time it was in the 2nd leaf position, and yet it retained the same maximum height.

The leaf did not subsequently (in March and April) bend over further between the 2nd and 3rd leaf positions.

In March and April the height of successive 2nd blades increased rapidly (Fig. 4.3.28) and they stood out above the younger and older leaves (Fig. 4.3.26). It follows that the angle between the 2nd blade and the vertical must have become more acute. The acuteness is further emphasised by the likelihood that successive blades at this time were less than twice the length of an average (half-emerged) first leaf (see section 4.3.3.3d, p.151).



Between late April and June the long 2nd leaves appear (Fig. 4.3.28) to have fallen over markedly as they aged to 3rd leaves. As a result the (younger) 2nd leaves still stood well out above the rest of the sward (Fig. 4.3.26).

In contrast, in July (1975), August and September (1974), 3rd leaves were remaining more erect (Fig. 4.3.28) and new leaves were beginning to grow to shorter heights. The 2nd and 3rd blades therefore tended to occupy the same depth of sward (Fig. 4.3.26).

REPRODUCTIVE TILLERS

(d) Heights of blades and stem in the sward

The vertical distribution of the leaf blades and stem on reproductive tillers is illustrated in Fig. 4.3.29. The values were obtained from reproductive tillers growing in the uncut swards in 1975.

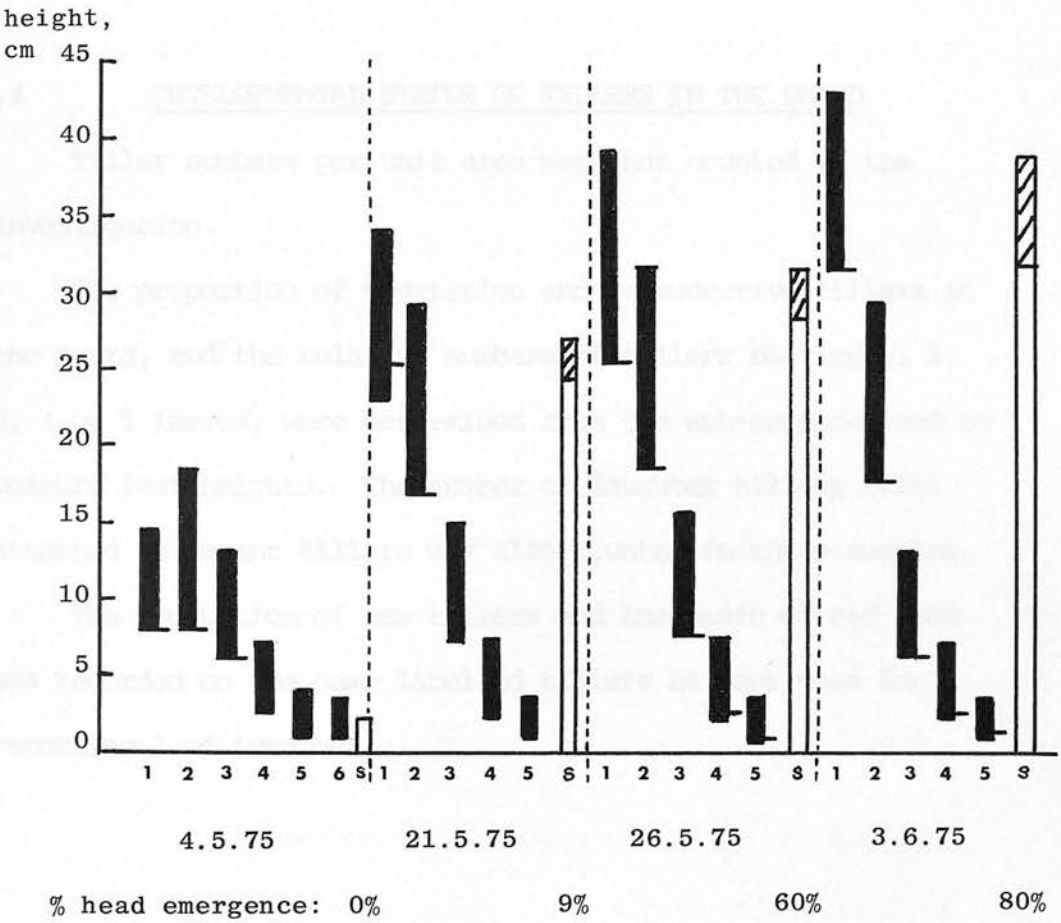


Fig. 4.3.29 : Vertical distribution of blades and stem on reproductive tillers in uncut swards.

leaf blade

stem + sheaths

height of ligule

emerged portion of stem + head

The mean height of emergence of the stem does not equal the mean ligule height of the 1st leaf when ear emergence is less than 100%; the numbers of observations are necessarily different.

It can be seen that as the stem elongated the leaf blades became spaced out into distinct zones. It is as though an internode continued to elongate until the ligule of the younger leaf was at the same height, or slightly higher, than the tip of the leaf below.

4.3.3.4 DEVELOPMENTAL STATUS OF TILLERS IN THE SWARD

Tiller numbers per unit area were not counted in the investigation.

The proportion of vegetative and reproductive tillers in the sward, and the relative numbers of tillers bearing 1, 2, 3, 4 or 5 leaves, were determined from the sub-samples used to measure leaf heights. The number of daughter tillers still attached to parent tillers was also counted in these samples.

The production of new tillers and the death of old ones was recorded on the same labelled tillers as were used for recording leaf turnover.

(a) Proportions of vegetative and reproductive tillers in the sward

Primary growth

Primary growth was not examined in 1974. In 1975, 43 ± 1.7% of the tillers in all plots were reproductive on May 5th, irrespective of the nitrogen treatment applied the year before. On May 26th, 42% of tillers in primary growth swards were reproductive and 49% on June 3rd. By July 1st 70% of the tillers growing in uncut swards (old N3 plots, unfertilized) were reproductive and there were many dead vegetative tillers present.

Regrowth

Cutting dates in 1974 and 1975 were not the same. On June 24th 1974 (30 days after the previous cut) the percentage of reproductive tillers was as follows:

N1	N2	N3	N4
6.7 ± *2.1*	18.9 ± *1.9*	29.1 ± *6.0*	28.5 ± *1.1*

On July 3rd 1975 (49 days after the previous cut), the percentages were little different from the previous year - allowing for the large S.E. in treatment N2:

N1	N2	N4
8.2 ± *0.9*	11.8 ± *4.4*	28.2 ± *1.2*

(b) Relative numbers of vegetative tillers bearing 1, 2, 3, 4 or 5 leaves

The proportions of tillers with 1, 2, 3, 4 or 5 leaves (alive or dead) per tiller are shown in Table 4.3.9. Unbiased estimates of leaf number per tiller could not be made from the January 17th, March 4th or June 4th 1975 tiller samples; on these occasions some of the leaves which might normally have been present had been removed in the last management cut. Results are presented as the average over all levels of nitrogen except where nitrogen appeared to have an effect.

Table 4.3.9 : Percentages of 1-, 2-, 3-, 4- and 5-leaved tillers making up the sward. Vegetative tillers, mean ± *S.E. (in italics)*

Date	N-LEVEL	% 1-leaved	% 2-leaved	% 3-leaved	% 4-leaved	% 5-leaved
24. 6.74	1	0 ± *0.0*	38 *3.3*	57 *4.0*	5 *3.9*	0 *0.0*
	2	1 *0.6*	27 *3.1*	65 *4.2*	6 *3.1*	1 *2.1*
	3	7 *3.0*	27 *4.8*	57 *3.8*	9 *1.0*	0 *0.0*
	4	6 *2.9*	29 *8.5*	52 *10.2*	13 *6.3*	0 *0.0*
	ALL N	3 *1.3*	30 *2.1*	57 *2.2*	8 *1.8*	0 *0.3*
14. 8.74	ALL N	1 *0.5*	19 *2.1*	50 *3.2*	28 *3.5*	1 *0.4*
2.10.74	ALL N	3 *1.1*	31 *1.9*	40 *2.0*	26 *2.3*	0 *0.2*
4. 4.75	ALL N	0 *0.0*	7 *1.8*	34 *2.4*	32 *4.3*	24 *4.6*
4. 5.75	ALL N	0 *0.0*	19 *4.5*	41 *2.7*	29 *2.7*	10 *3.3*
3. 7.75	1	0 *0.0*	3 *1.8*	29 *7.1*	44 *9.0*	23 *5.9*
	2	0 *0.0*	7 *1.8*	35 *7.9*	45 *8.1*	13 *2.4*
	4	0 *0.0*	11 *1.8*	43 *2.7*	39 *2.1*	7 *0.7*
	ALL N	0 *0.0*	7 *2.4*	36 *5.6*	43 *5.6*	14 *5.3*

A large proportion (33%) of tillers had only 1 or 2 leaves on 24.6.74 and 2.10.74. These may have been fairly recently produced tillers in which the third leaf had not yet developed.

By the end of the winter (4.4.75) many tillers (24%) were carrying 5 leaves. On July 3rd the majority of tillers again carried 3, 4 or 5 leaves. The proportions of 1 to 5 leaved tillers on July 3rd differed very markedly from those one year earlier on 24.6.74. A major management difference between the two occasions was the absence of a second cut in 1975.

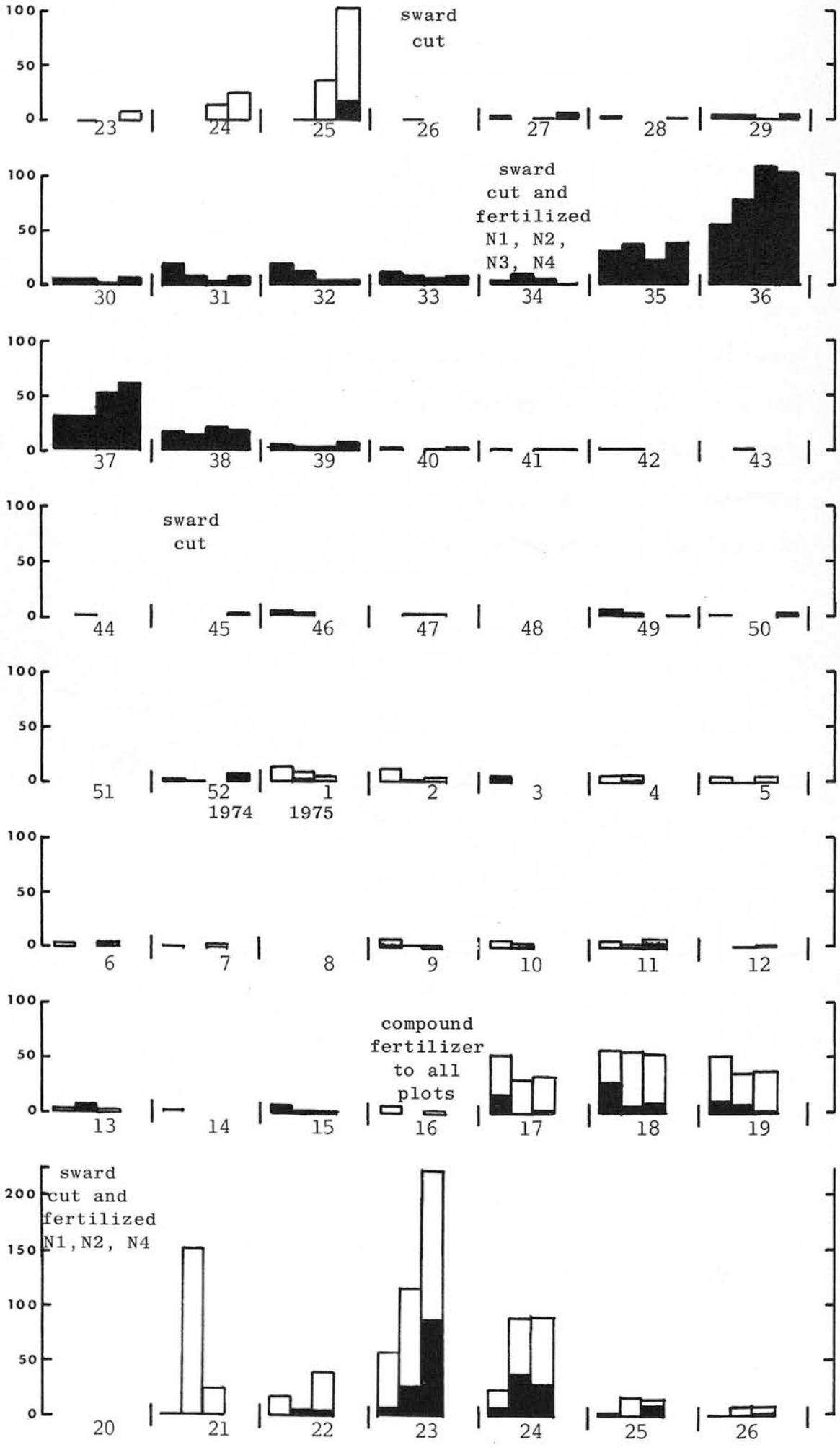
On the whole the amount of nitrogen applied had little effect on the proportions of 1, 2, 3, 4 and 5-leaved tillers. There were more 1-leaved tillers on the higher nitrogen plots on 24th June 1974 but the difference was not significant. On July 3rd the percentage of 2-leaved tillers increased with nitrogen level ($P < 0.05$).

The number of daughter tillers still attached to mature tillers in the foregoing samples are recorded in Table 4.3.10, expressed as a percentage of the total number of tillers making up the sample. Variation between replicates was large so the values for each replicate are given.

Table 4.3.10 : % of daughter tillers in sward

Date	N1			N2			N3			N4		
	R1	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3
25. 6.74	0	0	0	7	2	2	0	14	7	16	12	15
13. 8.74	7	9	15	11	2	2	2	7	4	7	11	15
2.10.74	0	15	23	23	5	20	25	11	11	14	11	18
17. 1.75	0	4	2							2	0	0
4. 3.75	0	0	0							0	0	5
4. 4.75	0	0	0							0	0	0
4. 5.75	2	0	0							2	0	0
4. 6.75	0	0	16	6	4	18				10	6	12
3. 7.75	6	0	0	0	4	0				2	0	0

The results suggest that nitrogen, particularly in 1974, led to increased tiller production following the fertilizer applications in May 1974 and May 1975. In July, August and September 1974 tillering took place to a similar extent under all nitrogen treatments, the mid-August fertilizer application not having a differential effect. Tillering in September was considerable. Little tiller production seems to have taken place over the winter or early spring, but began again in May. Few new tillers were produced during June 1975 compared to the previous year, as was suggested on P. 155 by observations on the proportions of 1- and 2-leaved tillers.


sward cut
sward cut and fertilized N1, N2, N3, N4
sward cut
compound fertilizer to all plots
sward cut and fertilized N1, N2, N4
1974
1975

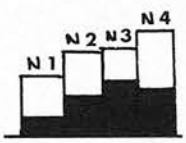
(c) Appearance of daughter tillers on ringed tillers

On the permanently marked tillers used for monitoring leaf appearance and death, subsidiary records were kept of the dates of appearance of daughter tillers. The observations are presented in Fig. 4.3.30.

The observations illustrate the larger flushes in tiller production following application of heavier levels of nitrogen fertilizer. However, since the sampling population was biased in tiller age (see p. 117), the actual rate of tillering cannot be extrapolated to the whole sward.

Fig. 4.3.30 : Numbers of daughter tillers emerging per week per 100 ringed tillers.

In 1974, successive blocks within a week represent nitrogen treatments N1, N2, N3, N4. In 1975, successive blocks within a week represent nitrogen treatments N1, N2, N4.



Week 1, 1974

Week 1, 1975

Shaded blocks represent daughter tillers appearing on vegetative tillers and (in 1975) on "suspected-reproductive" tillers (see section 4.3.2, p. 118). Unshaded blocks represent daughter tillers appearing on reproductive tillers.

(d) Deaths of ringed tillers

Deaths of labelled tillers occurred at a rate of 0 - 2% per week from mid-May to the end of July 1974, late August to early September 1974, and in the second week in May 1975. All these times coincided with periods of reproductive tiller development. At all other times the rate of death was 0 to 0.5% per week. Again these rates refer to a set of tillers generally older than the sward population and take no account of daughter tillers competing for light, etc.

4.3.3.5 WEIGHT OF DRY MATTER ABOVE GROUND LEVEL

The dry weight of material per unit area, including loose litter, was measured from ground level on all occasions when the structure of the sward was analysed - except on December 17th 1974. The results are given in Table 4.3.11.

Table 4.3.11 : Herbage dry weight, including loose litter, above ground level. Kg ha^{-1}, mean ± *S.E. (in italics)*

Date	Nitrogen level N1	N2	N3	N4
7. 5.74	2804 all plots *105*			
24. 6.74	2830 *198*	3329 *369*	4555 *436*	5100 *145*
14. 8.74	3056 *186*	2859 *296*	3245 *174*	3362 *142*
2.10.74	3726 *183*	3881 *168*	4128 *140*	4530 *126*
6.11.74	3117 *429*	3157 *251*	3384 *266*	3700 *185*
17. 1.75	1211 *48*			1127 *35*
4. 3.75	1030 *37*			1068 *37*
7. 4.75	1244 *41*			1391 *43*
5. 5.75	2464 *81*			2841 *73*
7. 6.75	1335 *72*	2150 *110*		2579 *124*
6. 7.75	2716 *124*	6022 *164*	(10,578) (PRIMARY GROWTH) *279*	7751 *213*

CHAPTER FIVE

EXPERIMENT 2

An experiment to examine the effect of the removal of particular leaves from the tiller on senescence (estimated by digestibility changes), and on regrowth, using three growth room environments.

5.1 INTRODUCTION

In section 3.3.2 it has been suggested that animals tend to remove only part of the shoot material, and that this tends to be the younger, more accessible, leaves. In consequence the number of leaves on a defoliated tiller will be temporarily out of balance - at first because the younger leaves are reduced or missing, and later the older leaves are absent because of earlier removal.

The effects of differential leaf removal can be expected to affect plant regrowth through a number of mechanisms: hormone production, carbon assimilation, size of sinks for assimilates, redistribution of mineral elements. Because of the number of insufficiently understood regulating mechanisms involved, it would be difficult to predict the effect of partial defoliation on the regrowth and quality of the pasture. The relative importances of leaf position, and number of leaves removed can, however, be ascertained by imposing differential defoliation treatments and measuring the responses. Investigations of this type have been conducted by A. DAVIES (1974) and DE LUCIA SILVA (1974), both with S24 ryegrass.

Removal of one leaf,or part of it, had no effect on production. Removal of two or more leaves including at least one young leaf reduced relative growth rate (see also ANSLOW, 1968), leaf appearance rate, relative tillering rate and the proportion of available tillering sites which produced tillers. Complete defoliation reduced these parameters considerably further, but removal of third and older leaves had no effect (see also BEGG & WRIGHT, 1964).

The results of DAVIES and DE LUCIA SILVA appear to differ in one respect in that DE LUCIA SILVA found a significant reduction in all growth parameters after removal of the third youngest leaf, whereas DAVIES did not. However, as DE LUCIA SILVA's treatments always included partial or complete removal of the second youngest leaf as well, his conclusion that the removal of the third leaf had an important effect on regrowth cannot be substantiated. The effect of partial defoliation on senescent tissue was also investigated by DE LUCIA SILVA but no clear effect of leaf removal on rate of senescence was found.

Some of the physiological consequences of partial defoliation have already been mentioned in Section 3.3.3:

(1) The removal of the two youngest leaves may severely reduce the supply of assimilate to the terminal meristem (p.76);

(2) Export of current assimilate from remaining leaf material is considerably increased (p.78);

(3) The decline in photosynthetic rate of leaf tissue remaining may be delayed (pp.78 and 79);

(4) Recirculation of mineral elements is prevented when older leaves are missing (p.82);

(5) There is some evidence that senescence may be delayed (GIFFORD & MARSHALL, 1973).

The experiment which follows was set up to examine the effect of defoliation at different leaf positions on rates of senescence (in terms of digestibility). Regrowth was also measured in terms of leaf weights, lengths, rate of production, tiller numbers and plot yields.

The experiment was carried out at three different termperatures in order to examine the effects of temperature on digestibility and tiller growth.

5.2 MATERIALS AND METHODS

5.2.1 MATERIALS AND THEIR PREPARATION

Swards of S24 perennial ryegrass were grown from seed in a greenhouse and then outdoors. They were then transferred to growth rooms where they were left to grow until three new leaves had developed on each tiller under the environmental conditions of the experiment.

5.2.1.1 GRASS SWARDS

Twenty mini-swards of S24 Aberystwyth Perennial Ryegrass were grown from seed in boxes 0.188 m^2 in area and 17.5 cm deep. The boxes were lined with polythene to cut down evaporation from the sides. Large drainage slits were cut in the bottom. The boxes were filled uniformly with layers of gravel (5.0 Kg), rubble (2.3 Kg) and riddled soil (25.4 Kg). At the beginning of February seed was scattered evenly on the surface and covered with a thin layer of fine soil.

The boxes were placed in a greenhouse until mid-April. At six weeks of age the swards were cut to 4 cm using battery-powered Wilkinson shears, and Nitram fertilizer was applied in solution at the rate of 67 Kg N ha^{-1}.

In mid-April the swards were cut to 4 cm again and transferred outdoors until the end of May. At the end of May, 250 Kg ha^{-1} of Fisons Extra Grass 29-5-5 (73 Kg N ha^{-1},

12.5 Kg P ha^{-1}, 12.5 Kg K ha^{-1}) was applied in solution. Twelve boxes were then moved into two of the growth rooms and the experiment commenced. Three weeks later 6 more boxes from outdoors were moved into the 3rd growth room.

5.2.1.2 GROWTH ROOMS

The growth rooms were insulated cabinets 1.80 m wide, 2.82 m long and 2.44 m high. The benches, 2.75 m × 0.9 m, were made of expanded metal through which air could circulate. The walls were lined with white plastisol. Each room had a thermostatically controlled cooling or heating system, a humidifier, a humidity controller capable of maintaining the humidity above a pre-set level, and an adjustable bank of 20 fluorescent tubes. Time clocks controlled photoperiod and the daytime-nighttime temperature regime.

The effects of defoliation were to have been observed under constant environmental conditions to minimise variation from sources other than the defoliation treatments. The defoliation treatments were examined under three temperature regimes:

(a) Temperature

The daytime temperatures selected were based on the relationship between rate of leaf appearance and temperature observed by MITCHELL (1956-7) in New Zealand perennial ryegrass (see Fig. 3.2, p. 19).

Rate of change in leaf production per week occurs rapidly at the lower end of the temperature range and plateaus out at about 20°C. Daytime temperatures of 5°, 10° and 20° were selected.

It was necessary to reduce the temperature of the 20° room at night to cut down respiration losses. This was done bearing in mind the low level of light intensity achieved in the experiment and therefore the suboptimal rate of photosynthesis that would occur. All rooms were set at 5°C at night.

The temperatures of the growth rooms during the experiment oscillated between plus and minus 1°C of the following temperatures:

Growth room	1	5.6°C	day	;	2.7°C	night
"	" 2	9.8°C	"	;	4.3°C	"
"	" 3	19.3°C	"	;	4.4°C	"

These were the temperatures actually achieved in the experiment when the controls were set at 5°C, 10°C and 20°C by day and 5°C by night.

(b) Light Intensity

Twenty 125 W warm white Crompton fluorescent tubes, 2.4 m in length, were suspended at a height of 17 cm above the surface of the sward to give the same light intensity in each room.

This was the first experiment to be carried out in new growth rooms and it was discovered during the course of the experiment that the light given out by the tubes was both less, and declined faster in time, at lower temperatures (see Fig. 5.2.1). As a result of this, differences in growth between chambers cannot simply be ascribed to temperature.

Light intensity was measured in each growth room towards the end of the experiment when it became apparent that the intensity given out by the tubes was different in each growth room. It was measured again after the end of the experiment, using new tubes, in order to determine the initial intensity of light in the rooms at the start of the experiment.

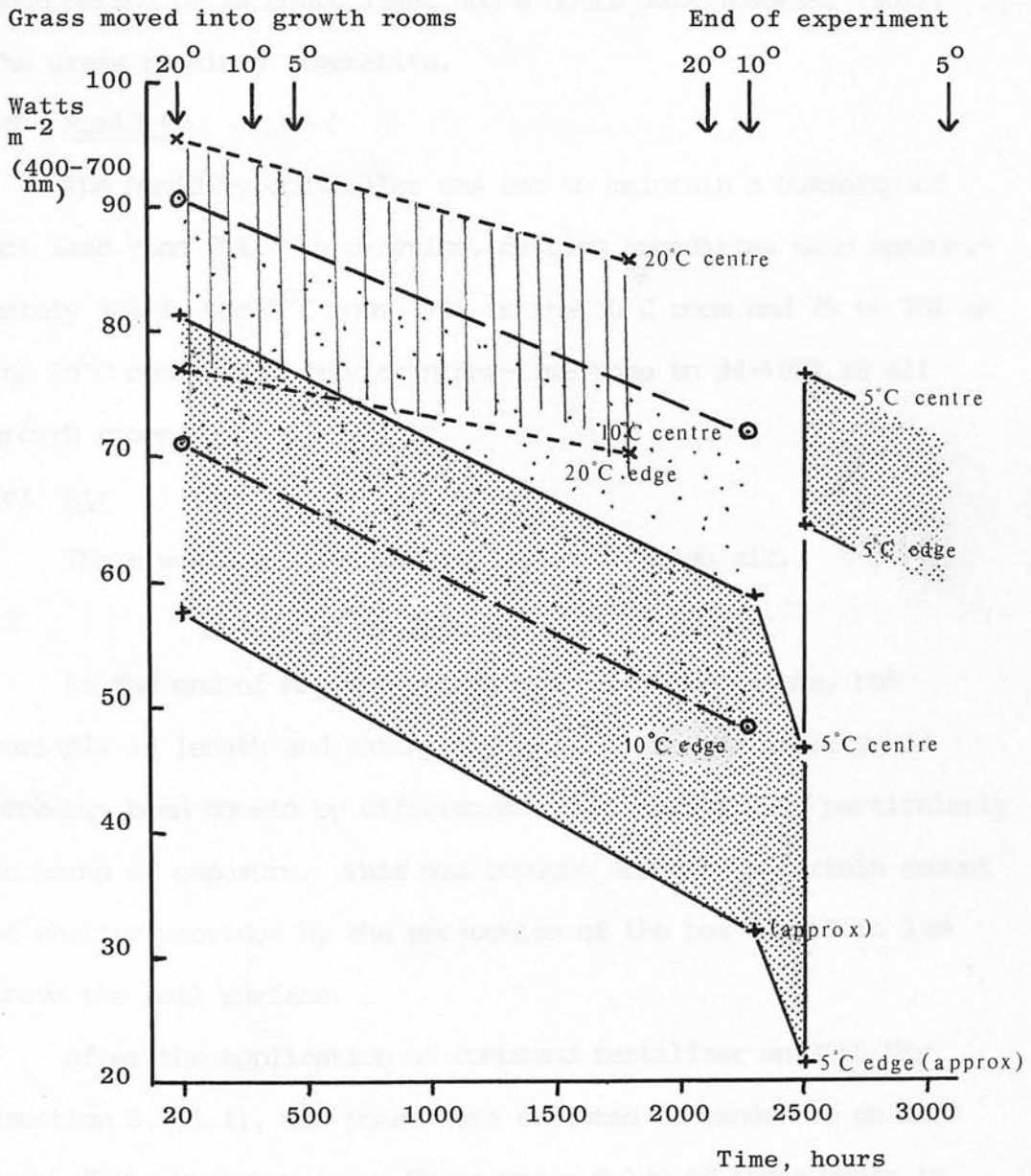


Fig. 5.2.1 : Initial levels of light intensity (W m^{-2}, 400-700nm) and rate of fall of intensity with time, in the 5°C, 10°C and 20°C rooms. Upper boundary shows intensity at centre of bench, lower boundary shows intensity at outer edge of boxes.

The tubes have a lifespan of about 2,500 hours. Those in the 5°C room had to be replaced 5 weeks before the end of the experiment.

Variation in intensity across the bench was counteracted by rotating the boxes.

(c) Photoperiod

Vernalisation of the tillers was avoided by imposing a long photoperiod of 16 hours light and 8 hours dark (COOPER, 1951). The grass remained vegetative.

(d) Humidity

The humidity controller was set to maintain a humidity of not less than 70%. In practice, daytime humidities were approximately 80% in the 5°C room, 70% in the 10°C room and 75 to 70% in the 20°C room. Humidity at night-time rose to 94-100% in all growth rooms.

(e) Air

There was a continual circulation of fresh air.

5.2.1.3 CONDITIONING PERIOD IN GROWTH ROOMS

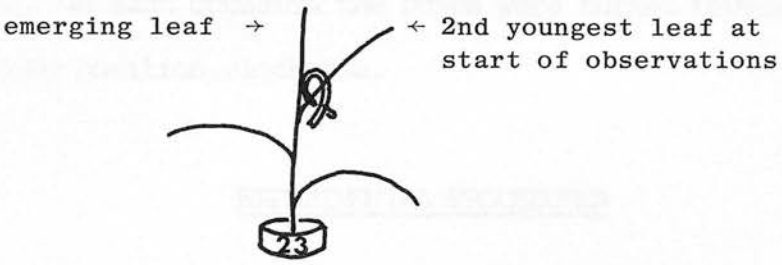
At the end of May the swards were short and dense, but variable in length and patchy in colour. The variability had probably been caused by differences in micro-climate, particularly in terms of exposure. This was brought about by a certain amount of shelter provided by the projection of the box edge 2 to 3 cm above the soil surface.

After the application of compound fertilizer on 30th May (section 5.2.1.1), six boxes were selected at random to go into each of the growth rooms. There was a delay of three weeks in transferring boxes to the 20°C room as the environmental controls were not working satisfactorily.

On being placed in the growth rooms the swards were subjected to a pretreatment period of adjustment.

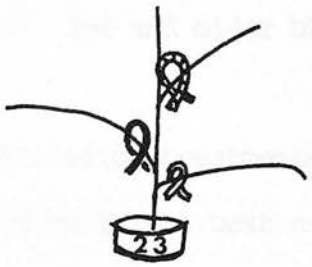
Leaf appearance records

Leaf appearance was monitored during the pretreatment period on 60 tillers in each room. Ten tillers per box were pinpointed from a random number grid and labelled with numbered rings made from red plastic tubing. The second-youngest leaf was marked with a small orange ring made out of fine plastic-coated telephone wire.



Tiller labelled for leaf appearance observations at start of pretreatment period.

Each labelled tiller was examined at least once every 10 days. If a new leaf had appeared, the date was recorded and a telephone-wire ring of another colour was hung on to the leaf below. A defined sequence of colours was used.



Labelled tiller two new leaves later.

Length of conditioning period

The grass was allowed to grow undisturbed until all the green and green/brown leaves present had grown under the environmental

conditions of the experiment. The length of this period was defined as the time taken for three new leaves to have developed per tiller.

Routine management of swards during conditioning period

The grass was watered to field capacity whenever the soil began to dry out. Once a week 10 Kg N ha^{-1} was applied as a solution of Nitram.

The boxes were rotated to counteract the uneven distribution of light intensity across the bench. They were moved three times a week. On each occasion the boxes were turned through 180^{o} and moved one position clockwise.

5.2.2 EXPERIMENTAL PROCEDURES

5.2.2.1 LAYOUT OF DEFOLIATION TREATMENTS

Six defoliation treatments were imposed in each growth room:

I No defoliation (control)

II 1st (youngest, elongating) blade removed - emerged portion of blade only

III 2nd (1st fully expanded) blade removed

IV 1st and 2nd blades removed

V Complete defoliation

VI 3rd and older blades removed

The defoliation treatments were applied on one occasion only, referred to in the text as DD, defoliation day.

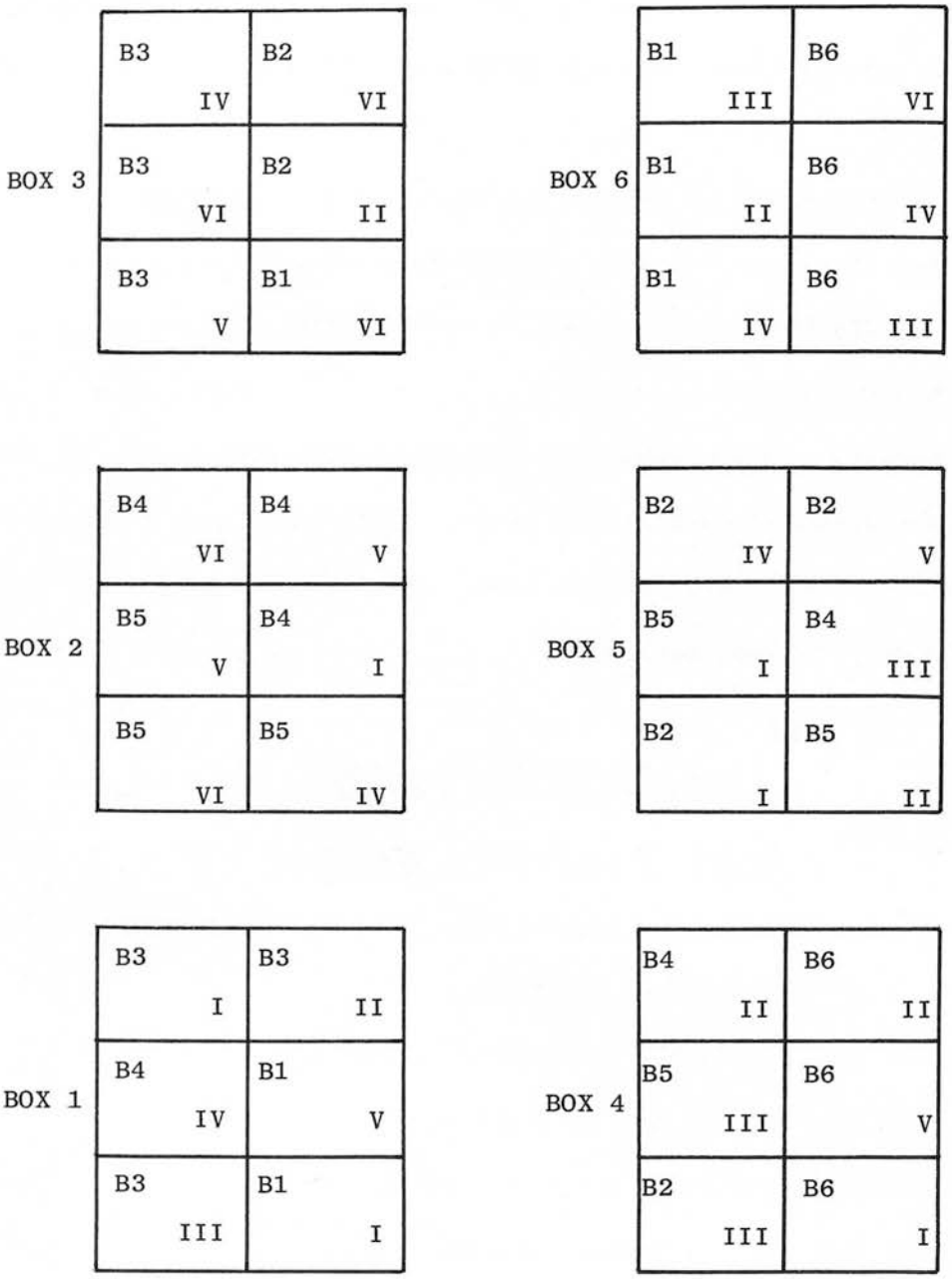


Fig. 5.2.2 : Layout of defoliation treatments in 10^{o}C room.

B = Block Type:

B1 = Good 6 miniplots

B2 = Good medium 6 miniplots

B3, B4, B5 = {Medium + Medium Poor $\frac{16}{2}$} = 3 × 6 miniplots

B6 = Poor 6 miniplots

Before the treatments could be applied, it was considered necessary to make some allowance for the variation in plant structure that was still apparent between boxes.

Accordingly, each of the six boxed swards in a growth room was divided by string into six mini-plots, giving a total of 36 mini-plots per growth room. The 36 mini-plots were matched on the basis of a visual score into 6 blocks; each block contained six mini-plots with similar visual scores. Within a block of matched mini-plots, the six defoliation treatments were allocated at random. Thus by blocking the mini-plots, the range of variation in growth appearance occurred equally in all defoliation treatments.

The layout of mini-plots and defoliation treatments in the $10^{o}C$ room is shown in Fig. 5.2.2.

5.2.2.2 ALLOCATION OF MINI-PLOTS TO SAMPLING DATES

One mini-plot contained sufficient dry weight for the *in vitro* digestibility analysis of leaf blades 1 to 4. Since the treatments were to be sampled on three occasions (1, 2 and 3 Leaf Appearance Intervals after defoliation), only half of the mini-plots for each treatment were required for destructive sampling. It was necessary to ensure that block type (visual growth score) was not confounded with sampling occasion when assigning mini-plots to sampling dates. This was dealt with as follows:

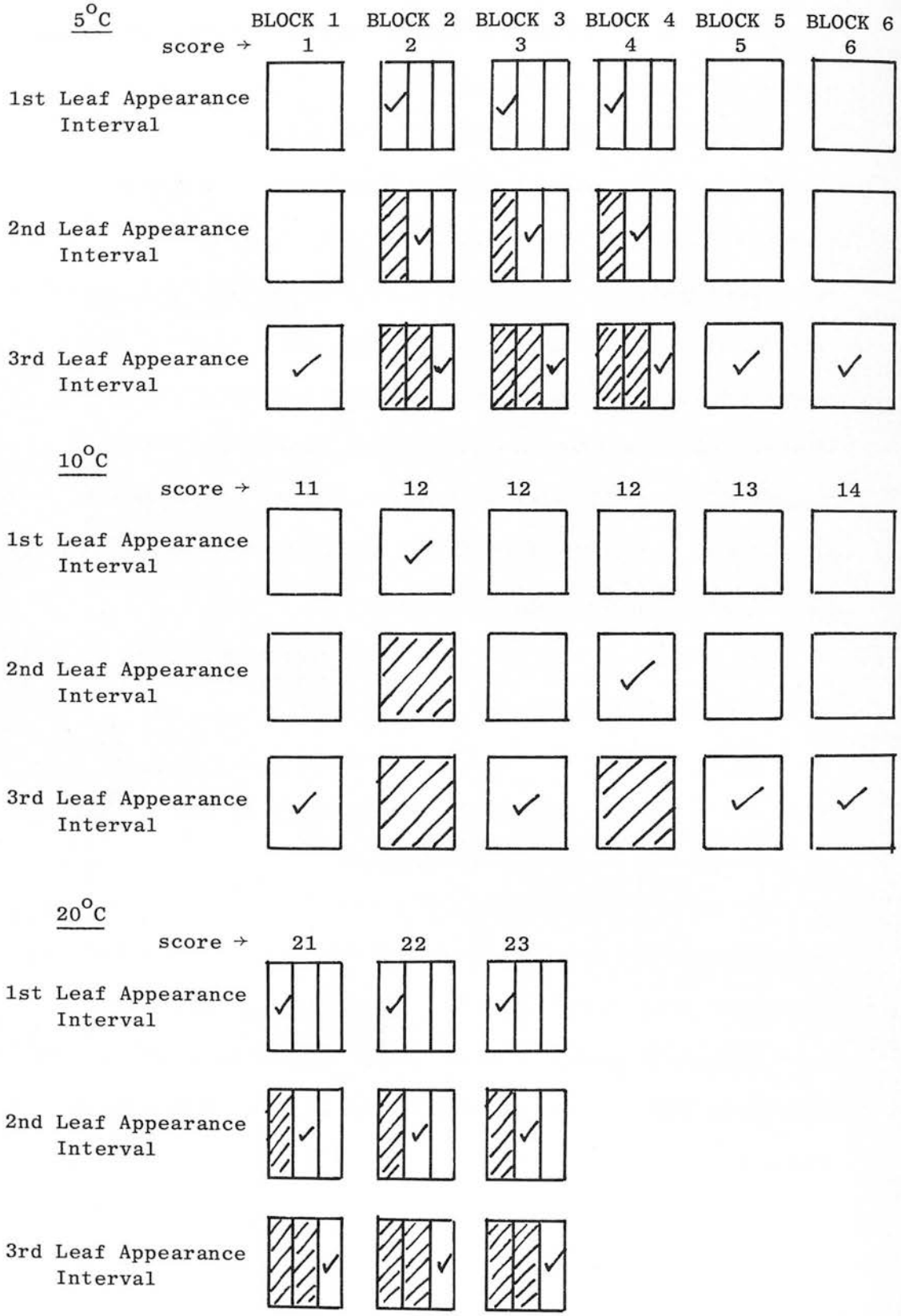


Fig. 5.2.3 : Scheme used in allocating mini-plot sampling areas to sampling dates. Tick shows area sampled.

In the 10°C room there were 18 mini-plots of similar visual score, (3 per treatment). Sampling occasions 1 to 3 were allocated at random to these three mini-plots and, when the sampling date arrived, the whole mini-plot was used. The three remaining mini-plots per treatment were all harvested on the 3rd sampling date to provide additional information.

In the 5°C and 20°C rooms there were fewer mini-plots of similar visual score. In the 5°C room the three blocks with intermediate visual scores were selected for destructive sampling. One third of each mini-plot was harvested on each sampling occasion, giving a total harvested area of one mini-plot per treatment per sampling date. On the 3rd sampling occasion, the 3 remaining mini-plots of more extreme visual growth score were also harvested for additional information.

In the 20°C room, the same procedure was adopted as in the 5°C room to spread mini-plot variation equally between sampling occasions. Only 3 mini-plots per treatment were defoliated in the 20°C room so there was no additional sampling of more extreme plots on the 3rd sampling date.

The sampling scheme is shown diagrammatically in Fig. 5.2.3 for one defoliation treatment.

5.2.2.3 IMPLEMENTATION OF TREATMENTS

Knitting needles were used to define successive narrow transects across a plot. The operator worked from one end of the transect to the other using a pair of fine-pointed scissors to remove the appropriate leaf/leaves from each tiller in turn. The complete defoliation treatment was easily dealt with by

trimming all the grass in the plot to a uniform height such that only very short stubs, if any, remained on each tiller.

It took about five days for four people to implement all the defoliation treatments within one growth room.

Preliminary observations

Whilst the treatments were being applied, tiller counts were carried out and samples collected for *in vitro* digestibility analysis. In the 20°C room, blade lengths and weights were also measured.

Initial tiller counts were done on all treatment III plots before defoliation. Permanent transects 2 cm × 20 cm were laid down the long centre of each plot using string. The number of tillers in each transect was counted, breaking up the count into single tillers, tillers with 1 daughter, tillers with 2 daughters, etc., and 'dead' tillers.

Samples of 1st, 2nd, 3rd and older blades were collected as defoliation proceeded. They were classified according to Growth Room temperature (e.g. 10°C), growth type (e.g. Block 1, visual score 'good') and leaf position (e.g. 2nd leaf). The samples were dried at 85°C and stored for *in vitro* digestibility analysis.

At the outset of the experiment, the appearance of the grass in the 20°C room differed considerably from that in the other two rooms. In the 20°C room there were up to 10 spiky hard leaves on each tiller, most of them brown; the green leaves were a light lime-green colour. In the 5°C and 10°C rooms there were four or five soft leaves per tiller; the green leaves were a rich deep hue. Between growth rooms, visual categories were not comparable.

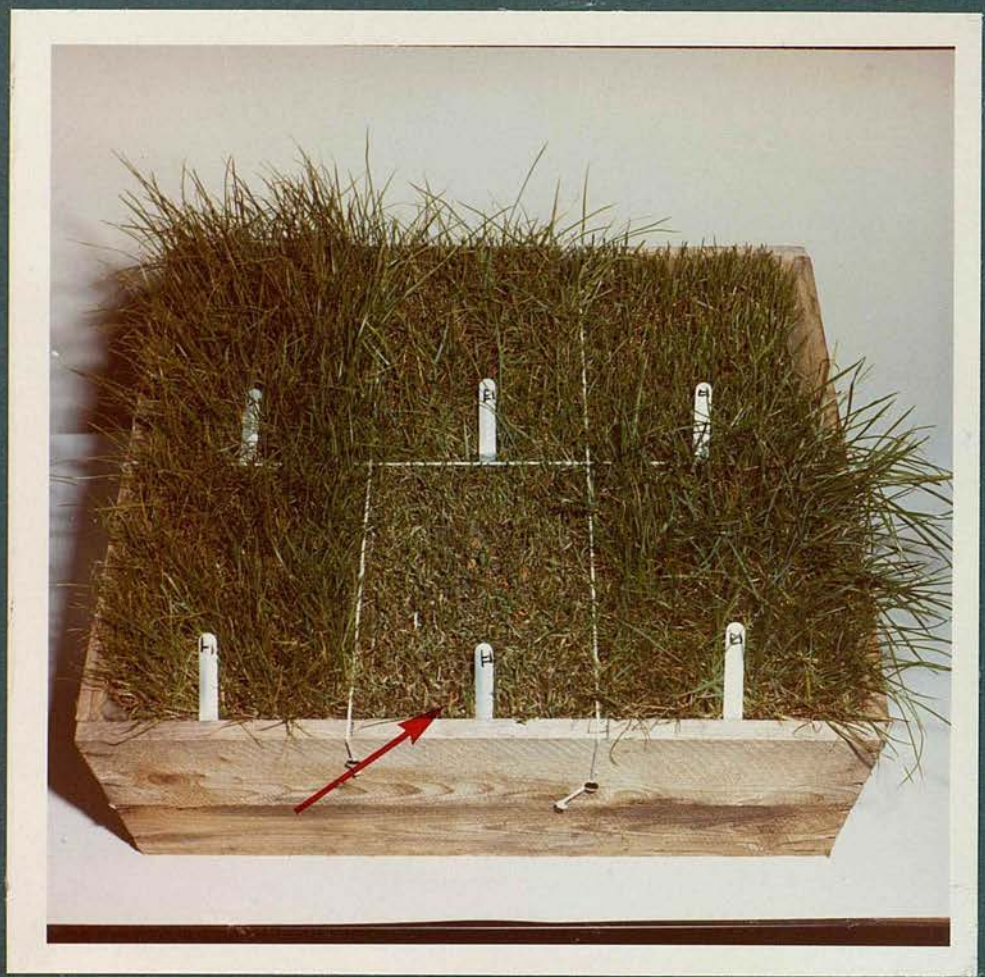


Fig. 5.2.4 : Layout of a boxed sward following defoliation.

Treatment codes do not correspond to those used in the text. I (in photo) = I (in text); II = V; III = IV; IV = III; V = VI.

Orange and red wire loops are just visible: they mark the tillers used for observations on leaf appearance.

5.2.2.4 LABELLING OF TILLERS FOR LEAF-APPEARANCE RECORDS

When defoliation had been completed, permanently labelled tillers were selected in each plot, as follows, to monitor the rate of leaf appearance. Sixty tillers per treatment, i.e. 10 tillers per plot, were used. Ten telephone-wire rings, all of the same colour, were scattered over the plot, avoiding a 2 cm border around the edge of the box. The rings were shaken to the base of the sward. The tiller nearest to the twisted ends of the wire was slipped through the ring. A ring of a different colour was hung on the second leaf. Where the second leaf had been removed it was necessary to wait until the stub remaining had extended before hanging a ring on it.

5.2.2.5 ROUTINE MANAGEMENT OF SWARDS POST-DEFOLIATION

Management was continued as in the pretreatment period (section 5.2.1.3) except that watering took place regularly three times a week for the 20°C room, and twice a week for the 5°C and 10°C rooms. Water was applied evenly over all the plots until they reached field capacity, when water began to run out of the bottom of the boxes.

Temperature and humidity were monitored throughout the pretreatment and experimental period using a Casella T9150-58 Thermo-hygrograph.

A non-systemic insecticide was sprayed on all the swards on two occasions to kill aphids.

SAMPLING

5.2.2.6 TIMES OF SAMPLING

Sampling of each treatment in each growth room took place on four occasions, from an area that had not been harvested previously.

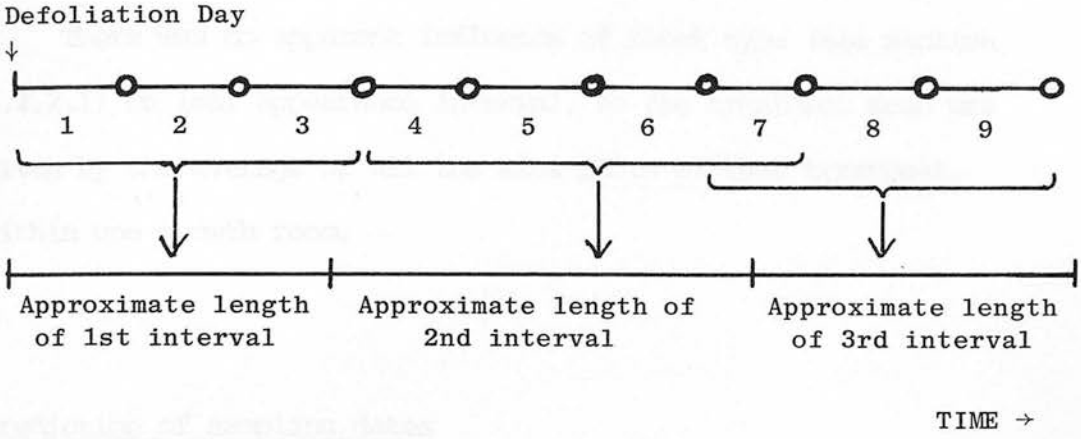
Sampling occasion	Measurements made
(1) At the time of defoliation	Tiller counts; *In vitro* digestibilities of blades 1 to 3. Blade lengths and weights, 20°C room only.
(2) After the first leaf appearance interval	Dry matter yield Lengths; } of blades 1 to 3; Weights; } and of older *In vitro* digestibilities; } blades where Age (from leaf appearance records); } sufficient material available.
(3) After the 1st + 2nd leaf appearance intervals	As in (2)
(4) After the 1st + 2nd + 3rd leaf appearance intervals	As in (2), plus: Tiller count; Leaf number per tiller; Colour of the youngest to oldest leaves; Remaining unharvested plots Tiller count Leaf number Leaf colour Yield

Dates of sampling were based on leaf appearance intervals within each treatment. Samples were taken at the time of defoliation and after one, two and three new leaves had grown on a tiller following defoliation.

Determination of the leaf appearance interval

The leaf appearance interval was determined from observations on the number of new leaves that had appeared on a set of marked tillers in a given length of time. The interval of time between successive recordings will be referred to as an "observation period". Where a new leaf had appeared, the leaf below was marked by hanging a coloured ring on it; a defined sequence of colours was used so that all the first leaves to appear had one colour of ring, all the second had another colour, and so on. At the beginning of the post-defoliation period, 10 marked tillers were available on all the mini-plots for scoring of leaf appearance. With successive harvests, the number of marked tillers remaining that could be used for this purpose was obviously reduced.

The 1st, 2nd and 3rd leaf appearance intervals were calculated for each mini-plot using leaf counts from observation periods that fell approximately within the specific interval being calculated. This is shown diagrammatically as follows:



'o' represents a day when a count of new leaves was made;

o——o represents an observation period.

In this example, the 1st interval was calculated from the first three observation periods; the 2nd interval from the next four; and the 3rd interval from the seventh to ninth observation periods.

The leaf appearance interval was thus given by the total number of tiller-days observed within the appropriate observation periods, divided by the total number of new leaves counted:

$$\text{Leaf appearance interval (in days)} = \frac{\sum_{i=1}^{n} t_i d_i}{\sum_{i=1}^{n} l_i} \qquad \ldots \qquad (1)$$

where n = number of observation periods during leaf appearance interval

i = observation period 1 to n

t_i = number of tillers examined in period i

d_i = number of days in observation period i

l_i = number of new leaves that had appeared in period i

There was no apparent influence of block type (see section 5.2.2.1) on leaf appearance interval, so the treatment mean was given by the average of all the mini-plots of that treatment, within one growth room.

Prediction of sampling dates

Sampling dates were fixed about half of a leaf appearance interval in advance, in order to plan labour requirements. It was therefore necessary to base the sampling date on a lagged estimate of the current leaf appearance interval. Observations on leaf appearance that had been made since half-way through the previous interval were substituted into equation (1) to give the estimated length of the current interval.

The first sampling date was fixed for each treatment separately as:

$$S_1 = DD + E_1$$

where S_1 = first sampling date

DD = defoliation day

E_1 = estimated 1st leaf appearance interval.

Half-way through the 2nd interval, the actual length of the 1st leaf appearance interval (L_1) was calculated from observations made between defoliation day (DD) and sampling date 1 (S_1). As before, an estimate was made of the 2nd leaf appearance interval (E_2).

Then the second sampling date was given by:

$$S_2 = DD + L_1 + E_2$$

where S_2 = second sampling date

DD = defoliation day

L_1 = actual length of 1st leaf appearance interval

E_2 = estimated length of 2nd leaf appearance interval.

Similarly, the third sampling date was given by:

$$S_3 = DD + L_1 + L_2 + E_3$$

where S_3 = third sampling date

L_2 = actual length of 2nd leaf appearance interval

E_3 = estimated length of 3rd leaf appearance interval.

5.2.2.7 SAMPLING PROCEDURE

The mini-plots to be sampled were given by the sampling scheme as outlined in section 5.2.2.2. The following procedure was carried out for each of these mini-plots, or $^1/_3$-mini-plots:

(1) Before the tillers were harvested tiller numbers, leaf colour and number of leaves per tiller were recorded. These records were made on the last sampling occasion only.

Tillers were counted within a transect $2 \times 20\ cm^2$ down the length of the mini-plot (10° and $20^{\circ}C$ rooms) or $3 \times 14\ cm^2$ across the mini-plot ($5^{\circ}C$ room). Tillers were categorised as single, single + 1 daughter, single + 2 daughters, etc., and dead. 'Dead' tillers, however, were not always clearly recognizable.

Leaf colour was noted for each leaf on each of 10 tillers. Three categories were used - green (50 - 100% green), 1 - 50% green, and brown. At the same time, the number of leaves on each tiller was counted. The 10 tillers examined were either those ringed for leaf appearance records, or, if too few of these remained, additional tillers were located at random.

(2) A 2 cm border was marked off on those sides of the mini-plot which were enclosed by the box edge, to eliminate any edge effect. The border was cut to ground level and used to determine the % dry matter of the herbage.

Dry matter yield of the mini-plot was recorded. First the area to be harvested was measured, then the grass was cut at ground level and weighed fresh. Dry matter yield was calculated using the % dry matter as estimated from the discarded border material.

(3) The fresh material from each harvested mini-plot was stored in polythene bags in a refrigerator for not more than 24 hours. Each sample was dealt with as follows:

The tillers were mixed around in the bag before withdrawing a subsample of 50. These tillers were separated into their component parts: 1st leaf (youngest), 2nd leaf, 3rd leaf, etc. and the numbers in each category were counted.

The sheaths were removed from the 2nd and 3rd leaves before measuring the lengths of those blades.

Both fresh and dry weights were determined for each separated category. The samples were dried at 85^{o}C for 24 hours.

The remaining tillers were separated into the same component parts as in the subsample. The sheaths of the 2nd and 3rd leaves were removed as these can differ considerably in digestibility from their blades (see Experiment One). The separated parts were dried at 85°C for 24 hours, added to the corresponding weighed portions of the subsample, and stored dry at room temperature in monocontainers.

The samples were analysed for *in vitro* dry matter and organic matter digestibility using the 2-stage technique of TILLEY & TERRY (1963) as modified by ALEXANDER & McGOWAN (1966).

Supplementary sampling of extra plots

Those plots which were not allocated within the main sampling program, were sampled at the end of the experiment as a further assessment of variability present within treatments.

Tiller counts, leaf colour and number of leaves per tiller were recorded as in 5.2.2.7(1). Dry matter yield was measured as in 5.2.2.7(2).

5.2.3 STATISTICAL ANALYSES

The experiment comprised 3 Growth Rooms (GR) with six Defoliation Treatments in each (TR), sampled at three successive Leaf Appearance Intervals post-defoliation (LI). Within each Growth Room a Treatment was applied to six blocks (5°C room and 10°C room) or three blocks (20°C room). The 20°C room was not sampled at the 2nd LI due to lack of time.

Digestibilities were determined from one block on each sampling occasion (10°C), or one bulked sample from three blocks (5°C and 20°C):

		TR					
		I	II	III	IV	V	VI
GR	LI						
1	1	1	1	1	1	1	1
(5°C)	2	1	1	1	1	1	1
	3	1	1	1	1	1	1
2	1	1	1	1	1	1	1
(10°C)	2	1	1	1	1	1	1
	3	1	1	1	1	1	1
3	1	1	1	1	1	1	1
(20°C)	2	1	0	0	0	0	0
	3	1	1	1	1	1	1

The entries in the table refer to the number of blocks or bulked blocks sampled.

Leaf lengths and weights were measured on one block (10°C) and three blocks (5°C and 20°C) per sampling occasion:

		TR					
		I	II	III	IV	V	VI
GR	LI						
1	1	3	3	3	3	3	3
	2	3	3	3	3	3	3
	3	3	3	3	3	3	3
2	1	1	1	1	1	1	1
	2	1	1	1	1	1	1
	3	1	1	1	1	1	1
3	1	3	3	3	3	3	3
	2	3	0	0	0	0	0
	3	3	3	3	3	3	3

Leaf appearance observations were maintained in each block throughout the experiment, except in the 10°C room where one block was lost at each sampling occasion:

		TR					
		I	II	III	IV	V	VI
GR	LI						
1	1	6	6	6	6	6	6
	2	6	6	6	6	6	6
	3	6	6	6	6	6	6
2	1	6	6	6	6	6	6
	2	5	5	5	5	5	5
	3	4	4	4	4	4	4
3	1	3	3	3	3	3	3
	2	3	3	3	3	3	3
	3	3	3	3	3	3	3

Plot yield was measured at the 1st and 2nd LI on the same number of samples as Leaf lengths and weights. Plot yield, leaf colour and tiller density were determined at the 3rd LI on all the remaining unharvested plots:

		TR					
		I	II	III	IV	V	VI
GR	LI						
1	3	6	6	6	6	6	6
2	3	3	3	3	3	3	3
3	3	3	3	3	3	3	3

Analysis of variance was used to separate out the relative effects of Growth Rooms, Leaf Appearance Interval and Defoliation Treatments. With the leaf appearance interval observations, block type was shown to have no effect on the values observed and was therefore used to provide replicates for each Treatment.

A three-factor Analysis of Variance was carried out between GR × LI × TR.

All of the other dependent variables measured in the experiment were lacking in observations from the 20°C room at the 2nd LI (see p.195). For all other measurements it was therefore necessary to perform three separate two-factor Analyses between combinations of GR × LI, GR × TR and LI × TR. If one of the independent variables was found to have a significant effect, it could not then be used to provide replicates in a two-factor Analysis of Variance between the other two independent variables; such an Analysis was discarded.

Main effects were not orthogonal, due to unequal replication. As a result, the variances calculated for each factor were not independent and a real significance in one factor could lead to an apparent significance in the other. The three 2-way Analysis of Variance tables therefore had to be examined in relation to one another. In almost all sets of observations examined, there was at least one factor which had no effect upon the dependent variable, so in practice it was possible to assess the relative significance of each main effect.

When Analysis of Variance showed that a factor had a significant effect on the variable measured, then Duncan's New Multiple Range Test was used to test differences between pairs of means. Because of unequal replication, the following procedure was adopted to determine the best possible estimate of variance in the circumstances:

(1) The Analysis of Variance tables based on the original individual observations were examined for the presence of

interactions between GR, LI and TR. Thus if TR pairs were to be tested and TR interacted with LI but not GR, then 2-way Analysis of Variance between TR and GR was selected. However, because replication was unequal, the residual mean square would have been weighted by some cells more than others.

(2) To overcome this bias, a second Analysis of Variance was carried out on the means of the observations from each cell; in this way, each cell was represented by only one value. The residual mean square from this analysis was then used as the estimate of variance (s^2) for Duncan's Multiple Range Test.

The number of degrees of freedom associated with s^2 was used as the number of degrees of freedom in Duncan's Test.

Subsequent procedure followed that described by STEEL & TORRIE (1960), p.107. An example is given below:

To test differences between Defoliation Treatments in 1st Leaf weight (mg).

GR \ TR	I	II	III	IV	V	VI	GR totals	GR means
1	3.73	4.13	3.97	2.97	3.07	4.27	22.14	3.69
2	3.97	3.43	3.63	3.10	2.40	3.33	19.86	3.31
3	3.50	3.15	3.75	2.75	2.60	3.25	19.00	3.17
TR totals	11.20	10.71	11.35	8.82	8.07	10.85	61.00	
TR means	3.73	3.57	3.78	2.94	2.69	3.62		

Analysis of Variance

Source of Variation	SOS	df	MS	F
GR	0.880	2	0.440	5.93
TR	3.149	5	0.630	8.49
Residual	0.742	10	0.074	
Total	4.771	17		

$s^2 = 0.074$

s, for comparing TR means = $\sqrt{\frac{s^2}{3}}$

s, for comparing GR means = $\sqrt{\frac{s^2}{6}}$

Significant Studentized Ranges for 5% and 1% level of protection, with 10 df :

N	2	3	4	5	6
SSR 0.05	3.15	3.30	3.37	3.43	3.46
SSR 0.01	4.48	4.73	4.88	4.96	5.06
LSR_N 0.05	0.50	0.52	0.53	0.54	0.54
LSR_N 0.01	0.70	0.74	0.77	0.78	0.80

where N = number of ranked means over which a comparison is being made,

SSR 0.05 = Significant Studentized Range at 5% level of protection,

LSR 0.05 = Least Significant Range at 5% level of protection,

= SSR $\times \sqrt{\frac{s^2}{3}}$ for TR means.

Treatments ranked :

V	IV	II	VI	I	III
2.69	2.94	3.57	3.62	3.73	3.78

III - V = 1.09 , > 0.80 (LSR_6,0.01) $\therefore$ P < 0.01

III - IV = 0.84 , > 0.78 (LSR_5,0.01) $\therefore$ P < 0.01

III - II = 0.21 , < 0.53 (LSR_4,0.05) $\therefore$ N.S.

III - VI = 0.16 , < 0.52 (LSR_3,0.05) $\therefore$ N.S.

III - I = 0.05 , < 0.50 (LSR_2,0.05) $\therefore$ N.S.

Repeating this comparison procedure for all pair-wise combinations of TR gives the following groupings :

V	IV	II	VI	I	III
a	a	b	b	b	b

where Treatments with the same case letter are not significantly different from one another.

5.3 RESULTS. EXPERIMENT 2

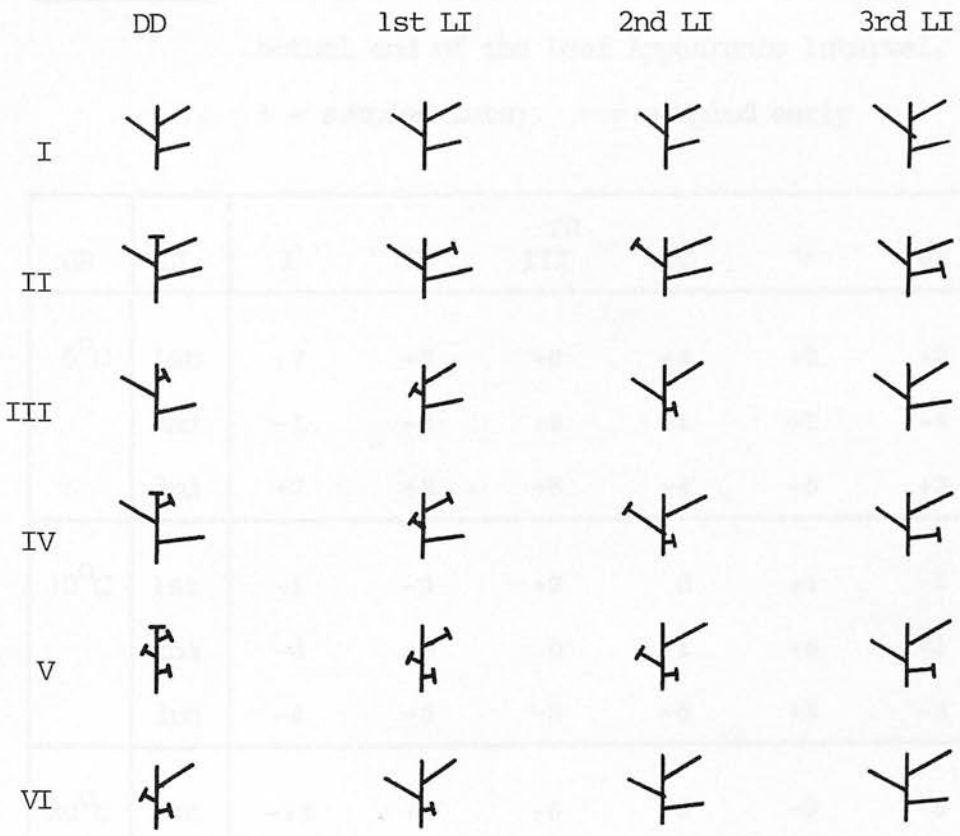
5.3.1 SYMBOLS USED AND DEFOLIATION TREATMENTS

GR	Growth Room
1st GR	$5^{o}C$ Growth Room
2nd GR	$10^{o}C$ Growth Room
3rd GR	$20^{o}C$ Growth Room
LI	Leaf Appearance Interval post-defoliation
1st LI	End of the 1st leaf appearance interval - i.e. time when, on average, one new leaf had appeared per tiller since defoliation.
2nd LI	End of the 2nd leaf appearance interval
3rd LI	End of the 3rd leaf appearance interval
DD	Day on which defoliation treatment was applied
1st LI - DD	Length of the 1st leaf appearance interval
2nd LI - 1st LI	" " " 2nd " " "
3rd LI - 2nd LI	" " " 3rd " " "
TR	Defoliation Treatment
I	Control - no defoliation
II	1st (emerging) blade removed (emerged portion only)
III	2nd (youngest fully emerged) blade removed
IV	1st and 2nd blades removed
V	Complete defoliation
VI	3rd and older blades removed

TR•GR	One treatment in one growth room
TR•LI	One treatment at one leaf appearance interval
LI•GR	One leaf appearance interval within one growth room
TR•GR•LI	One treatment in one growth room at one leaf appearance interval after defoliation.

Defoliation Treatments

The diagram below shows which blades were present (|), cut on average to half their length (|) (cut while emerging), and completely or almost completely removed (|).



5.3.2 SAMPLING DATES

Samples were collected for leaf length, weight and digestibility measurement 1, 2 and 3 Leaf Appearance Intervals after defoliation.

The length of the leaf appearance interval was predicted as described on p. 186. The discrepancy between the predicted sampling date and the actual end of the leaf appearance interval is shown in Table 5.3.0.

Table 5.3.0 : Number of days between sampling date and the actual end of the Leaf Appearance Interval.
+ = sampled late; - = sampled early

GR	LI	TR I	II	III	IV	V	VI
5°C	1st	+7	+3	+6	+4	+5	+3
	2nd	-1	-4	+2	-1	+1	-4
	3rd	+7	+3	+6	+4	+5	+3
10°C	1st	-1	-2	+3	0	+1	-1
	2nd	-4	0	0	+1	+5	-1
	3rd	-4	-5	-2	-6	+2	-3
20°C	1st	-14	+2	-6	-3	-3	-5
	2nd	-6					
	3rd	-5	+1	+1	-1	-2	-2

5.3.3 CONDITIONS OF THE EXPERIMENT

5.3.3.1 ENVIRONMENTAL CONDITIONS

Daytime temperatures and light intensities differed between Growth Rooms. Details have been given on pp. 175-178 and are summarised below.

Temperature

	Day	Night
GR 1 ('5°C' room)	5.6°C	2.7°C
GR 2 ('10°C' room)	9.8°C	4.3°C
GR 3 ('20°C' room)	19.3°C	4.4°C

Light Intensity

The amount of photosynthetically active radiation (400 - 700 nm) incident on the surface of the swards declined during the course of the pretreatment and experimental periods, particularly in the 5°C and 10°C rooms.

Approximate amount of radiation (400 - 700 nm) incident on the swards, Wm^{-2}.

	Start of pretreatment period		End of experiment
GR1	67	47 (half-way through 3rd LI)	72-67 (tubes replaced)
GR2	80	-	64
GR3	90	-	79

Light intensities in the growth rooms were similar to those outdoors in December and January in Britain (80 Wm^{-2} is approximately equal to 7 cal cm^{-2} hr^{-1}) but since the photoperiod

was twice as long (16 hours compared with 7 to 7½ hours outdoors, see p. 113) the total amount of radiation received in a day was more similar to that received in mid-November and February (HOGG, 1971).

Light intensity and temperature in the 6°C/3°C room were thus fairly similar to that found in December and January outdoors, but the photoperiod (16 hours) was twice as long.

The 10°C/4°C and 19°C/4°C environments bore no resemblance to field conditions. Light intensities were one-half to one-third of those in April and October, and one-quarter of that in June.

The decline in light intensity as fluorescent tubes age, and the reduction in intensity emitted at lower temperatures, were both unforeseen. In order to counteract the decline in intensity with time, a mixture of partially-used and new tubes should be used, the older tubes being periodically replaced by new ones to maintain the original light level (DOWNS & HELLMERS, 1975, p. 42).

A similar light intensity at different temperatures can be provided by one of two methods according to the cost and light intensity acceptable. Either the number of tubes used at the higher temperatures can be reduced, or the lamps can be partitioned off from the rest of the chamber by perspex so that the temperature of the air surrounding them can be regulated independently of the rest of the chamber.

5.3.3.2 NATURE OF THE SWARD

The swards were very dense seedling swards, most tillers being single while a few carried one, two or three daughter tillers. The number of tillers per unit area (see section 5.3.7.5, p. 232) was between two and seven times the numbers that have been recorded in the field.

The conditions of the experiment differed from those in the defoliation experiments of A. DAVIES and DE LUCIA SILVA (see p.172). DAVIES and DE LUCIA SILVA were working with spaced plants grown in greenhouses. DAVIES' plants were grown in buckets of nutrient solution while DE LUCIA SILVA's were grown in pots of soil.

The difficulties encountered with light intensity in the growth rooms, the low intensity of light in the 10°C and 20°C rooms in relation to day-time temperature, and the very dense nature of the seedling swards, all necessitate caution in interpreting the observations. Nonetheless, the results have provided some useful information on factors influencing digestibility, and tend to support those of A. DAVIES and DE LUCIA SILVA with respect to the effects of defoliation treatments on regrowth weight.

5.3.4 SUMMARY OF RESULTS

The results are presented in three main sections. The first examines the rate of leaf turnover in terms of leaf appearance rate and number of live leaves per tiller. It shows that defoliation treatments had no effect on leaf appearance while there was a difference between growth rooms. There was evidence that defoliation stress prolonged the lifespan of leaves produced immediately after the stress was applied.

The second section examines the quality of the regrowth in terms of the digestibilities of leaf blades at successive positions on the tiller. Again defoliation treatments had no effect on digestibility but there were differences associated with the three environments, the 20°C room leading to very low digestibilities in younger leaves. Major change in leaf digestibility showed the

same association with loss of green colouration as was found in the field experiment. The rates of fall in digestibility between one leaf position and the next were also of similar magnitude to those measured in Experiment 1.

The third section examines the quantity of regrowth following defoliation. Severe defoliation treatments reduced the weights and lengths of leaves produced subsequently. Except in one treatment, weight per unit length was unaffected. Leaves were heavier at cooler temperatures and weight per unit length was considerably increased, particularly in the younger (2nd) blades.

A substantial number of tillers died in the 20°C room and this appears to have been inversely related to the penetration of light to the base of the sward in this particular environment. No explanation can be put forward for this.

5.3.5 LEAF APPEARANCE AND NUMBER OF LIVE LEAVES PER TILLER

5.3.5.1 LEAF APPEARANCE INTERVALS (Table 5.3.1)

Leaf appearance interval was determined in each mini-plot. Mini-plots had been blocked on the basis of a visual score of growth vigour. Analyses of Variance of Blocks against length of the leaf appearance interval showed that block type had no effect on leaf appearance rate within any of the growth rooms. Blocks were used as replicates for each TR·GR·LI.

3-way Analysis of Variance on TR × GR × LI showed that LI and GR had significant effects ($P<0.01$ and $P<0.001$ respectively) on the leaf appearance interval, but TR had none. The interaction between GR and LI was also significant ($P<0.001$); interactions between TR × LI and TR × GR were not.

Table 5.3.1 : Length of the leaf appearance interval for the 1st, 2nd and 3rd leaf appearance intervals after defoliation, (days). *S.E. given in italics.*

GR	Appearance Interval after defoliation	I	II	III	IV	V	VI	Interval mean
5°C	1st	26 *1.2*	25 *2.4*	25 *1.4*	26 *0.7*	25 *1.4*	28 *1.9*	26.2 *0.6*
	2nd	36 *3.0*	42 *3.8*	36 *1.9*	40 *2.1*	36 *2.3*	40 *3.1*	38.1 *1.1*
	3rd	40 *9.3*	37 *3.9*	34 *2.3*	42 *4.8*	45 *4.6*	37 *3.1*	39.2 *1.8*
10°C	1st	25 *1.2*	23 *1.3*	27 *2.3*	28 *2.0*	28 *1.5*	25 *1.7*	26.4 *0.8*
	2nd	26 *1.4*	21 *4.1*	22 *0.4*	23 *0.7*	23 *1.9*	25 *0.6*	23.2 *0.7*
	3rd	29 *1.5*	28 *3.9*	26 *1.3*	26 *2.3*	27 *1.3*	27 *1.2*	27.1 *0.7*
20°C	1st	34 *5.0*	20 *0.9*	26 *4.6*	26 *2.4*	26 *2.5*	26 *4.4*	26.0 *1.6*
	2nd	21 *1.4*	15 *1.0*	19 *0.3*	18 *0.8*	14 *2.0*	16 *0.6*	17.2 *0.7*
	3rd	18 *3.2*	16 *1.1*	15 *0.2*	14 *1.0*	12 *0.8*	15 *0.7*	15.0 *0.7*
Treatment mean		28.3	26.2	27.0	25.6	26.6	25.2	

Leaf Appearance Interval

When the grass was first moved into the growth rooms, the length of time between the appearance of successive leaves was about 11 days. Immediately prior to defoliation, the leaf appearance interval was 28.2, 20.4 and 19.2 days in the 5°C, 10°C and 20°C rooms respectively. The Interval means for each Growth Room in Table 5.3.1 suggest that tillers in the 5°C and 20°C rooms were still adapting to environmental conditions when the defoliation treatments were applied.

Duncans Multiple Range Test was carried out between successive LI for the 5°C and 20°C rooms separately. The estimate of variance was obtained from the residual mean square in Analyses of Variance between LI and TR for each growth room. In the 5°C room the 1st leaf appearance interval was significantly shorter than the 2nd and 3rd intervals ($P<0.01$). In the 20°C room the 1st leaf appearance interval was longer than the 2nd ($P<0.01$) and the 2nd was, in turn, longer than the 3rd ($P<0.05$).

The slow adjustment in leaf appearance rate is surprising in view of the rapid response in leaf extension rate to changes in temperature (WILLIAMS & BIDDISCOMBE, 1965). It was expected that a pretreatment period of three leaf appearances would be sufficient for the plants to adapt to the conditions of the experiment (e.g. see MITCHELL, 1956-7).

The effect of Growth Rooms on leaf appearance is best examined at the 3rd LI only, since plants were adjusting in leaf appearance rate until at least the 3rd LI in the 20°C room. The leaf appearance interval was 12 days longer in the 5°C room than in the 10°C room, and a further 12 days longer in the 10°C room than in the

20°C room. (5°C : 39 days, 10°C : 27 days, 20°C : 15 days).

Fig. 5.3.1 shows these results expressed as leaves appearing per tiller per week :

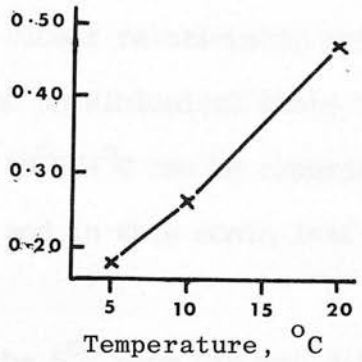


Fig. 5.3.1

Leaf appearance rates were more than twice as slow as those measured in growth rooms by MITCHELL (1956-7, New Zealand perennial ryegrass, see p. 19), COOPER (1964, three contrasting climatic races of perennial ryegrass), SILSBURY (1970, *L. perenne* cv. Grasslands Ruanui) and PEACOCK (1975c, S24 perennial ryegrass).

Three reasons for the slow rates of leaf appearance in this experiment can be considered, *viz* low light intensities, cold night-time temperatures, and high tiller densities.

SILSBURY (1970) suggests from his review that leaf appearance rate may be limited by low light intensity of the order of 20 to 100 Wm^{-2}. Such light intensities were used both here and by COOPER, SILSBURY and PEACOCK; nonetheless they still obtained much higher rates of leaf appearance.

It may be that the cold night temperature imposed in this experiment led to the slow rate of leaf appearance. Except in the low temperature rooms, such cold night temperatures were not imposed in the experiments of MITCHELL, COOPER, SILSBURY or

PEACOCK. WILLIAMS & BIDDISCOMBE (1965) found that the rate at which leaves extended was more closely correlated with night temperature than with mean daily temperature. Their correlation could, however, merely reflect a closer relationship with a third factor such as daylength and physiological state of the plant. The temperature range of 19°C/4°C can be experienced outdoors in May (PEACOCK, 1975c) and in this month leaf appearance rate is rapid.

The climatic conditions of the 5°C room did not differ substantially from those provided by other experimenters at that temperature, and yet a slow rate of leaf appearance (1 leaf in 39 days) was obtained. This compares with 22 days reported by COOPER (1964) and about 14 to 22 days by MITCHELL (1956-7). Thus although it is possible that cold night temperatures might be responsible for slow rates of leaf appearance in the 10°C and 20°C rooms, the slow rate in the 5°C room suggests that some other factor must have been involved. SILSBURY (1970) reports that KLOOT (1967) demonstrated a marked decrease in leaf appearance rate at high plant densities.

It appears, then, that high tiller density may have had a substantial effect in reducing the rate of leaf appearance at least in the 5°C room. The influence of low light intensity or low night temperature on rates in the 10°C and 20°C rooms may have been relatively less important.

INTERPRETATION OF THE OTHER MEASUREMENTS IN THE LIGHT OF THE LEAF APPEARANCE INTERVAL RESULTS

Plants in the 5°C room were still adjusting to the conditions of the experiment between DD and the 1st LI; grass in the 20°C

room may still have been adjusting to that room by the 3rd LI. Caution must therefore be used when interpreting differences between Leaf Appearance intervals.

Where the results show an interaction between GR and LI, then further caution is required when comparing Growth Rooms. The effect of Leaf Appearance Interval has, therefore, always been examined first.

5.3.5.2 NUMBER OF LIVE LEAVES PER TILLER

The term 'live leaf' has been used here in the same way as in Experiment 1 to denote any leaf that had not yet turned 100% brown. Leaf colour was recorded at the end of the experiment on 10 tillers per mini-plot (30 tillers per Treatment in the 10°C and 20°C rooms, 60 per Treatment in the 5°C room). Each leaf was scored as more than 50% green, 1 - 50% green, or completely brown.

Table 5.3.2 : Number of leaves per tiller at the 3rd LI that were more than 50% green. *S.E. in italics.*

GR \ TR	I	II	III	IV	V	VI	GR means
5°C	2.38	2.50	2.27	2.43	2.52	2.58	2.45
	0.09	*0.07*	*0.10*	*0.08*	*0.07*	*0.08*	*0.03*
10°C	2.59	2.70	2.56	2.67	2.71	2.77	2.67
	0.12	*0.13*	*0.10*	*0.12*	*0.12*	*0.16*	*0.05*
20°C	2.70	2.77	2.67	2.87	2.73	2.87	2.77
	0.15	*0.14*	*0.15*	*0.14*	*0.08*	*0.12*	*0.05*
TR means	2.56	2.66	2.50	2.66	2.65	2.74	

Analysis of Variance showed that both Growth Rooms and Treatments influenced live leaf number per tiller ($P<0.001$ in each case).

The estimate of variance used to compare differences between growth room pairs and treatment pairs was obtained from the error mean square in a second Analysis of Variance between TR and GR; the Treatment mean was used rather than the individual observations in order to obtain a variance estimate unbiased by the different number of observations in each room (see pp. 194-195).

Duncans Multiple Range Test showed that there were fewer live leaves per tiller in the $10^{o}C$ room than in the $20^{o}C$ room ($P<0.01$), and still fewer in the $5^{o}C$ room than in the $10^{o}C$ room ($P<0.01$).

Defoliation treatments fell into three groups significantly different from one another ($P<0.05$) on the basis of the Multiple Range Test:

I and III	;	II, IV and V	;	VI	
2.50 to 2.56		2.65 to 2.66		2.74	live leaves $tiller^{-1}$

Those leaves which were senescing at the 3rd LI were those which had appeared during the 1st leaf appearance interval after defoliation. Thus in Treatments II, IV and V, the partial absence of the 1st to 2nd Blade (II) or 1st to 2nd Blade plus older leaves (IV, V), prolonged the lifespan of the emerging leaf. Absence of the 2nd to 3rd Blade only (III) had no effect on the lifespan of the emerging leaf, but absence of the 3rd to 4th plus older Blades (VI) appears to have prolonged the lifespan of the emerging leaf most of all.

The preceding results were number of live leaves per tiller (live = 1 to 100% green). A similar analysis was carried out on the number of green leaves per tiller (green = 50 to 100% green). These results are tabulated in Appendix 9.

The effect of Growth Rooms was again highly significant, but Defoliation treatments did not fall into distinct groups as before although the ranking order was almost the same. Thus defoliation treatments seem to have had a differential effect on the number of leaves which were 0 - 50% green, i.e. the older senescent leaves, but not the number of leaves which were 50 - 100% green. This may suggest that defoliation treatments only had a differential effect on the lifespan of leaves produced immediately after the stress was applied.

GIFFORD & MARSHALL (1973) suggest from their results that enhanced demand for assimilate (in their case by defoliated daughter tillers) delayed the normal decline of photosynthetic rate with age in main-shoot tissues. In Experiment 2, the leaf tissue remaining and the expanding new leaf may have responded in a similar manner to the removal of leaves most active in supplying the terminal meristem with assimilate (Treatments II, IV and V) (see Appendix 2).

This mechanism would not account for an increased lifespan in the emerging leaf following removal of the 3rd and older leaves. It is a matter of conjecture whether the latter effect might have resulted from an upset in some hormonal balance between emerging and senescing leaves (see pp. 15 - 16 of Literature Review).

Table 5.3.3 : *In vitro* organic matter digestibilities of 1st Leaf. *S.E.'s given in italics.*

1ST LEAF

GR	LI	I	II	III	IV	V	VI	Interval mean
5°C	DD	82.8 *0.8*						
	1st	85.8 *0.8*	87.6 *0.6*	85.0 *0.4*	83.6 *0.2*	86.8 *0.8*	88.0 *0.6*	86.1 *0.7*
	2nd	85.8	86.4	88.2	85.2	85.4	87.8	86.5 *0.5*
	3rd	86.4	87.8	87.8	87.8	87.4	86.0	87.2 *0.3*
10°C	DD	84.4 *0.4*						
	1st	83.2	83.2 *0.4*	86.4 *1.6*	84.2 *0.4*	82.8	83.4	83.9 *0.5*
	2nd	84.7	87.0	86.2	86.6	86.8	86.0	86.2 *0.3*
	3rd	86.6	85.2	87.6	87.0	87.2	86.8	86.7 *0.3*
20°C	DD	67.7 *0.8*						
	1st	71.2	74.8	73.8	71.4	72.2	72.2	72.6 *0.6*
	2nd	76.4						
	3rd	72.0	74.8	72.8	70.8	71.4	75.2	72.8 *0.7*
Mean of 5°C+10°C		85.4 *0.5*	86.2 *0.7*	86.9 *0.5*	85.7 *0.7*	86.1 *0.7*	86.3 *0.7*	

5.3.6 REGROWTH QUALITY

5.3.6.1 DIGESTIBILITIES OF THE 1ST LEAF, 2ND BLADE, 3RD BLADE, 4TH LEAF, AND OLDER LEAVES

(a) 1st Leaf Digestibility (Table 5.3.3)

Leaf Appearance Interval

1st leaf digestibility increased between DD and the 1st LI in the 5°C and 20°C rooms. After this, 1st leaf digestibility generally remained constant although there was an apparent difference between the 1st and 2nd LI's in the 10°C room.

Treatments

The defoliation treatments had no effect on 1st leaf digestibility.

Growth Rooms

The mean digestibility of the 1st leaf in each Growth Room could therefore be taken as the average over all Treatments in Leaf Appearance Intervals 1 to 3 (LI 1 and 3 only in 20°C room):

5°C	10°C	20°C
86.6 ± *0.3*	85.6 ± *0.4*	72.7 ± *0.5*

Duncans Multiple Range Test was used to test differences between Growth Rooms. The estimate of variance was provided by the residual mean square in an Analysis of Variance between GR and TR (averaged over all LI); there was no interaction between GR and TR.

1st leaves were more digestible in the 5°C room than in the 10°C ($P<0.05$). The difference was due to the rather low digestibilities measured in the 1st LI only, in the 10°C room, so it appears unlikely that there was a consistent real difference between the two rooms.

Table 5.3.4 : IVOMD of 2nd Blade.

S.E.'s given in italics.

2ND BLADE

GR	LI	I	II	III	IV	V	VI	Interval mean
5°C	DD	82.4 *0.6*						
	1st	82.4 *1.2*	82.8† *0.4*	81.0 *0.2*	80.8† *0.4*	81.8†	83.8 *1.0*	82.1 *0.5*
	2nd	82.0	82.6	83.8	82.0	83.4	83.2	82.8 *0.3*
	3rd	79.0 *0.8*	81.6	82.2	80.8	79.8 *1.8*	79.8	80.5 *0.5*
10°C	DD	83.0 *0.6*						
	1st	80.8	80.0† *0.7*	80.2 *1.4*	80.4† *0.6*	79.4†	77.4	79.7 *0.5*
	2nd	78.0	80.0	81.6	81.6	82.2	79.6	80.5 *0.6*
	3rd	79.4	80.0	82.6	80.8	84.2	81.4	81.3 *0.7*
20°C	DD	63.4 *0.6*						
	1st	61.8	66.4†	66.0	66.2†	67.2†	64.0	65.3 *0.8*
	2nd	67.4						
	3rd	67.4	65.4	68.2 *1.6*	65.6	63.6	65.6	66.0 *0.7*
Mean of 5°C+10°C		80.3 *0.7*	81.2 *0.8*	81.9 *0.2*	81.1 *0.5*	81.8 *0.5*	80.9 *1.0*	

† leaves cut when emerging

There was a marked difference (13.5 IVOMD units) in 1st leaf digestibility between the 20°C room and the two cooler rooms.

(b) 2nd Blade Digestibility (Table 5.3.4)

Leaf Appearance Interval

In general, digestibility of the 2nd blade did not differ between LI within Growth Rooms. An exception to this was the fall in 2nd blade digestibility in the 5°C room between the 2nd and 3rd LI. In the 5°C room, half of the 2nd blades (i.e. the older 2nd blades) at the 3rd LI were leaves which had emerged under a particularly low light intensity (see section 5.2.1.2(b), p. 177).

Treatments

Defoliation treatments in which the expanded portion of the emerging leaf was removed (II, IV and V) gave rise to 2nd blades cut to varying lengths at the 1st LI. The results show that removal of the expanded portion of an emerging leaf had no effect on the digestibility of that leaf one leaf appearance interval later.

It seems likely that the severity of defoliation had no effect on the digestibility of 2nd Blades subsequently produced. The effect of the severity of defoliation on digestibility (or on any of the other measurements), was assessed by comparing severe treatments IV and V with the less severe treatments II, III, VI, and with the control, I. Treatment means were calculated from all the observations on a treatment in the 5°C plus 10°C rooms. There was no difference in 2nd Blade digestibility between defoliation treatments.

Table 5.3.5 : IVOMD of 3rd Blade.

S.E. in italics.

GR	LI	I	II	III	IV	V	VI	Interval mean
5°C	1st	76.0 *3.6*	71.6	74.4 ††	66.8 ††			72.2 *2.0*
	2nd	70.6	68.0 †	73.6	65.2 †	73.6 †	74.6	70.9 *1.5*
	3rd	64.8	70.8	72.0	70.2	71.2	68.0	69.5 *1.1*
10°C	DD	79.3						
	1st	67.6	67.0 *1.8*	72.8 †† *3.0*	66.2 †† *3.8*	68.2 ††	59.0	68.4 * *0.9*
	2nd	63.6	69.2	72.5	69.2 †	69.8 †	69.8	69.0 *2.8*
	3rd	63.2	68.2	71.0	64.4	69.4	70.4	67.8 *2.2*
20°C	DD	59.9 *0.8*						
	1st	54.2	54.8	55.8 ††	52.2 ††		58.6	54.2 * *0.1*
	2nd	61.2						
	3rd	57.0	62.0	58.4	58.6	57.8	59.4	58.9 *1.0*
Mean of 5% + 10%		67.6 *2.0*	69.1 *0.7*	72.7 *0.5*	67.0 *0.9*	70.4 *0.9*	68.4 *2.6*	

† blade cut when emerging

†† blade cut when "fully" expanded - material consists of some younger and older blades which were not cut, plus some blade stubs.

* mean of treatments I - IV only, to balance with 5°C.

10°C, 1st LI, mean of I - VI = 66.8 ± *1.8*

20°C, 1st LI, mean of I - V = 55.1 ± *1.0*

Values from the 20°C room also suggest that defoliation treatments had no effect on 2nd blade digestibility.

Growth Rooms

The mean digestibility of the 2nd Blade in each Growth Room was calculated over all TR × LI values after Defoliation Treatments and Leaf Appearance Intervals had been shown to have little effect:

5°C	10°C	20°C
81.8 ± *0.3*	80.5 ± *0.4*	65.6 ± *0.5*

Duncans Multiple Range Test showed that the small difference in digestibility between the 5°C and 10°C rooms was significant (P=0.01).

2nd Blade digestibility in the 20°C room was about 15 units lower than in the 5°C and 10°C rooms.

(c) 3rd Blade Digestibility (Table 5.3.5)

Table 5.3.5 shows that the S.E.'s of the digestibilities of the 3rd Blade were large, reflecting the wide range in digestibility that leaves pass through as they age from the 2nd to the 4th leaf position.

Leaf Appearance Interval

3rd Blades present at the 1st LI had emerged during the pre-treatment conditioning period; those present at the 2nd LI were emerging at the time of defoliation. The one sample analysed for digestibility at DD in the 10°C room suggests that a major alteration occurred in 3rd Blade digestibility as plants became acclimatised to this environment. No evidence is available from the 5°C room. There was a similar, though smaller, fall in the 20°C room but the change was then

reversed between the 1st and the 3rd LI. 3rd Blade digestibility appears to have settled at a constant level after the 1st Interval post-defoliation in both the 5°C and 10°C rooms.

Treatments

In general, it appears that defoliation severity had no effect upon the digestibility of the 3rd blade (treatments IV and V compared with treatments I, II and VI).

The relative effects of the defoliation treatments within a leaf appearance interval cannot be evaluated because the standard errors were so large. This means that the senescence of 3rd blades, estimated by their relative digestibilities, cannot be examined in relation to the presence or absence of other leaves on the tiller. These large standard errors are partly a function of the large changes taking place in 3rd blades due to ageing, as mentioned above. Large standard errors were also obtained from senescing leaves in Experiment 1.

Digestibility analyses on 3rd blades from treatments III, IV and V at the 1st LI were carried out on cut stubs. The cut stubs were produced by further extention of the 2nd blade after it had been cut at the point of emergence (see section 5.3.7.3, p. 227). Treatment III (2nd Blade only removed) had a higher digestibility at the 1st LI (cut stub) and 2nd LI (leaf above cut stub) in both the 5°C and 10°C rooms, compared with other treatments. Leaf stubs from treatments where other leaves had been removed in addition to the 2nd blade (IV and V) did not show the same heightened digestibility as those from treatment III.

In order to interpret differences between stubs and intact leaves, it would be necessary to know how digestibility alters down the length of the leaf. Since leaves go brown at the tip first, the higher digestibility of the 3rd blade stub compared with an intact 3rd blade may simply reflect the difference in green colouration. It is curious that treatment III continued to show the highest digestibility at the 2nd and 3rd LI as well, in the 5°C and 10°C rooms, since it had the second lowest number of live leaves per tiller (p. 209).

In the 20°C room, treatment III 3rd blades did not have higher digestibilities than in other treatments.

Growth Rooms

Differences between Growth Rooms in 3rd blade digestibility have been assessed using values from the 2nd and 3rd LI only; 3rd Blades at the 1st LI were disqualified as they expanded during the pretreatment period. The mean for the 20°C room was derived from observations in the 3rd LI only. The inconsistency is not thought to prejudice the Growth Room comparison in view of the large difference between digestibilities in the 20°C room and the other two rooms:

5°C	10°C	20°C
70.2 ± *0.9*	68.4 ± *0.9*	58.9 ± *0.7*

On the basis of Duncans Multiple Range Test, there was no significant difference between the 5°C and 10°C rooms. The estimate of variance was derived from an Analysis of Variance on GR × TR (TR averaged over 2nd and 3rd LI; 3rd LI only in 20°C room).

3rd blade digestibility in the 20°C room is about 10 units lower than in the 5°C and 10°C rooms.

Table 5.3.6 : IVOMD of 4th Leaf.

S.E. in italics.

GR	LI	I	II	III	IV	V	VI	Interval mean
5°C	1st	52.6		47.5	47.0		51.0††	49.0* *1.8*
	2nd	50.2	45.4	49.8††	39.8††	40.0††	51.2	46.1 *2.1*
	3rd	46.4	49.8†	50.2	50.0†	48.4†	47.8	48.8 *0.6*
10°C	1st	50.4	48.8	47.5	49.4	37.0		49.1* *0.9*
	2nd	39.8	50.6	49.0††	34.2††	40.6††	50.0	44.0 *2.8*
	3rd	47.8	47.2†	54.6	39.2†	51.8†	52.0	48.8 *2.2*
20°C	DD	49.3 *0.8*						
	1st	43.0	39.8	43.0	43.2	36.0	50.8††	43.1* *0.1*
	2nd	50.8						
	3rd	44.8	49.8†	47.8	51.2†	49.0†	45.8	48.1 *1.0*
Mean of 5° + 10° + 20°		47.3 *1.4*	47.3 *1.4*	48.7 *1.2*	44.2 *2.2*	43.3 *2.4*	49.8 *0.8*	

† blade cut when emerging

†† blade cut when "fully" expanded - material consists mainly of sheaths.

* mean of treatments I, III, IV only.

5°C, 1st LI, mean of I, III, IV, V = 49.5 ± *1.4*

10°C, 1st LI, mean of I - IV, VI = 46.6 ± *2.5*

20°C, 1st LI, mean of I - VI = 42.6 ± *2.0*

(d) 4th Leaf Digestibility (Table 5.3.6)

S.E.'s of 4th leaf digestibilities are as large or larger than, those of the 3rd Blade.

The digestibility of the 4th Leaf was the same throughout the experiment except in the 20°C room at the 1st LI. This relative constancy in digestibility occurred in spite of the leaves having emerged at different times with respect to the pre-treatment and treatment periods. The 4th leaves present at the 1st and 2nd LI had expanded during the pre-treatment period. The 4th leaf at the 3rd LI had been expanding at the time of defoliation.

Differences between defoliation treatments cannot be examined closely since the presence of cut blades, blade stubs and sheaths in many of the samples complicate the interpretation too much. A tendency can be observed in Table 5.3.6 for the 4th leaf in the two severe defoliation treatments (IV and V) to be 3 or 4 units lower in digestibility than in the other treatments. Since the lowest values in treatments IV and V do not follow a consistent pattern, the reality of the difference remains open to question.

Growth Rooms

Growth Rooms have been compared using 4th leaf digestibilities from the 3rd LI only because earlier 4th leaves had expanded during the pre-treatment period.

5°C	10°C	20°C
48.8 ± *0.6*	48.8 ± *2.2*	48.1 ± *1.0*

There was no difference in digestibility between Growth Rooms by the time leaves had reached the 4th position on a tiller.

(e) Digestibilities of the 5th, 6th and 7th leaves (Table 5.3.7)

The 5th, 6th and 7th leaves grew outwith the experiment during the pre-treatment phase (5th and 6th leaves) or earlier (6th and 7th leaves). However, the opportunity of measuring the digestibilities of these leaves was taken: the older leaves remained attached to the tiller longer in the growth rooms than in the field so their ages in terms of leaf position were identifiable.

Table 5.3.7 : IVOMD of 5th, 6th and 7th leaves.

S.E. in italics.

Leaf position	LI	GR	
		5°C	20°C
5th	2nd		36
	3rd	37 ± *1.4*	36 ± *0.7*
6th	2nd		26
	3rd		26 ± *0.5*
7th	3rd		26 ± *1.2*

The 5th, 6th and 7th leaves were much lower in digestibility than the lowest standard used in *in vitro* runs for the 2nd experiment. The values quoted above are thus rather artificial, even more so when it is considered that they were digested without any nitrogen supplement or green herbage present.

The measurements do demonstrate, however, that the leaf material analysed had reached its lowest digestibility when it was 6 leaf appearance intervals old.

5.3.6.2 CHANGES IN DIGESTIBILITY OF LEAVES AS THEY AGED

The digestibility of a blade at one leaf position at one particular LI was subtracted from the digestibility at the previous leaf position one LI earlier. It was assumed that the digestibility of a 4th Blade was equal to that of a 4th Leaf (whose digestibility was measured). In the first experiment this assumption was shown to be reasonable on the only occasion it was measured (p. 141).

The results are tabulated in detail in Appendix 10. They show that digestibility fell to an increasing extent between the 1st and 2nd leaf positions in the 5°C room as the experiment progressed. Sections 5.3.6.1(a) and (b) show that it was the 2nd blade digestibility that decreased while 1st leaf digestibility remained high. Meanwhile the change in digestibility from 1st to 2nd blade in the 10°C room stayed the same throughout the experiment. It may or may not be pertinent to point out that by the 3rd LI there were fewer live leaves per tiller in the 5°C room than in the 10°C room.

The digestibility changes within Growth Rooms, averaged over all TR and LI, are shown in Table 5.3.8 and Fig. 5.3.2.

Table 5.3.8 : Decrease in digestibility of leaf blades as they aged (IVOMD units). *S.E. in italics.*

GR	1st Leaf → 2nd Blade		2nd Blade → 3rd Blade		3rd Blade → 4th Leaf		Total fall in digestibility
5°C	3.3	*0.59*	11.8	*0.85*	23.6††	*1.20*	38.7
10°C	4.3	*0.37*	13.2	*0.99*	21.8††	*1.95*	39.3
20°C	2.4†	*0.80*	8.2†	*1.05*	17.3†	*1.99*	27.9

†† observations from 2 Intervals only

† " " 1 Interval "

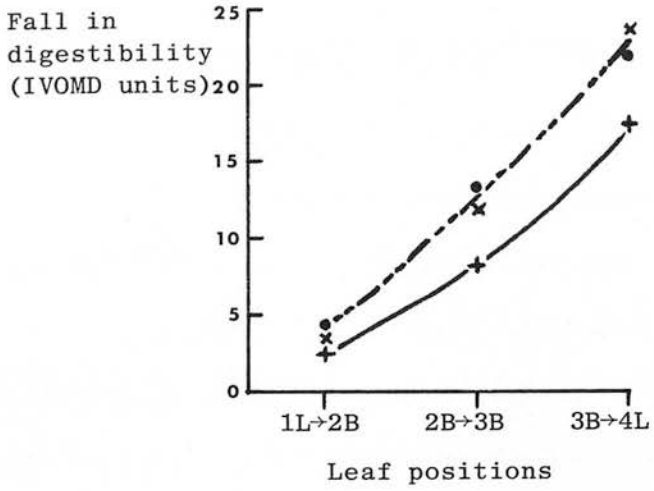


Fig. 5.3.2 : Fall in IVOMD between one leaf position and the next as leaves aged.

× = 5°C room; ● = 10°room; + = 20°room.

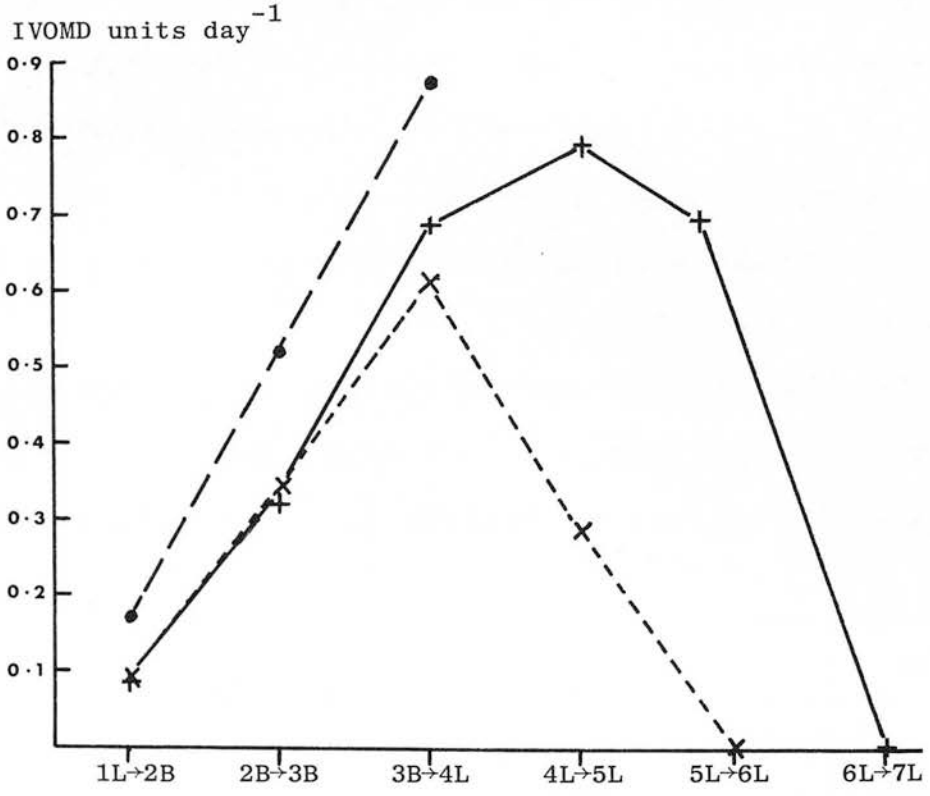


Fig. 5.3.3 : Rate of fall in IVOMD between one leaf position and the next. (IVOMD units per day.)

×---× = 5°C room; ●——● = 10°C room; +——+ = 20°C room.

Between the 1st and 2nd leaf positions the digestibility change was similar in all three growth rooms. Between the 2nd and 3rd, and the 3rd and 4th, leaf positions there was a rather smaller fall in the 20°C room than in the other two rooms.

Rate of change in digestibility

The rate of change in digestibility was calculated by dividing the length of the leaf appearance interval into the corresponding decrease in digestibility. The results for all TR·GR·LI are tabulated in Appendix 11. Table 5.3.9 shows the rate of change in digestibility within each Growth Room, averaged over all TR and LI. The results are plotted in Fig. 5.3.3 against Leaf Position, together with additional measurements made on older leaves in the 5°C and 20°C rooms - though these older leaves did not all emerge under the conditions of the experiment.

Table 5.3.9 : Rates of change in digestibility (IVOMD units per day). *S.E. in italics.*

GR	1st Leaf → 2nd Blade	2nd Blade → 3rd Blade	3rd Blade → 4th Leaf
5°C	0.09 *0.016*	0.34 *0.027*	0.61†† *0.036*
10°C	0.17 *0.014*	0.52 *0.038*	0.87†† *0.087*
20°C	0.09† *0.023*	0.32† *0.047*	0.68† *0.101*

†† 2 Intervals only

† 1 Interval only

5.3.7 REGROWTH QUANTITY

5.3.7.1 DRY WEIGHTS OF 1ST LEAF, 2ND, 3RD AND 4TH BLADES

The fresh and dry weights of 1st Leaf, 2nd Blade, 3rd Blade and 4th Leaf were determined at the end of each Leaf Appearance Interval. 50 tillers per sampling area (3 areas per Treatment in the 5°C and 20°C rooms, 1 area per Treatment in the 10°C room) were separated into the different leaf fractions. The fraction was weighed, dried at 85°C, and reweighed. Weight per leaf (or blade) was calculated by dividing the weight of the fraction by the number of leaves in it.

Some fractions were from positions where leaf blades had been partially or completely removed by the defoliation treatment. The mean weight per leaf was based on the number of leaves in that category that would have been present had they not been defoliated. The number of leaves absent as a result of defoliation was estimated by comparison with the control treatment (TR I).

Leaf weights are presented in Tables 5.3.10 to 5.3.13.

The 5°C and 20°C room weights are the means of three samples per treatment, whereas those of the 10°C room are from one sample per treatment per Leaf Appearance Interval.

(a) Weight of 1st Leaf (Table 5.3.10)

Leaf Appearance Interval

Analysis of Variance between LI × GR showed that there was a significant interaction ($P<0.05$) between the two factors. Weight of the 1st Leaf showed a small tendency to increase in the 10°C room and decrease in the 20°C room with successive LI.

Table 5.3.10 : Dry weight of 1st Leaf, mg.

S.E. given in italics.

GR	LI	I	II	III	IV	V	VI
5°C	1st	3.6 *0.44*	3.7 *0.33*	3.9 *0.44*	2.5 *0.02*	2.9 *0.38*	3.9 *0.32*
	2nd	4.0 *0.19*	4.5 *0.24*	4.3 *0.12*	3.1 *0.26*	3.1 *0.18*	4.6 *0.53*
	3rd	3.6 *0.31*	4.2 *0.49*	3.7 *0.13*	3.3 *0.42*	3.2 *0.16*	4.3 *0.26*
10°C	1st	3.3	2.6	3.7	3.3	2.2	3.0
	2nd	4.1	3.7	3.6	2.7	2.5	3.3
	3rd	4.5	4.0	3.6	3.3	2.5	3.7
20°C	1st	3.5 *0.28*	3.4 *0.67*	4.1 *0.33*	2.8 *0.28*	3.0 *0.07*	3.5 *0.31*
	2nd	2.4 *0.50*					
	3rd	3.5 *0.38*	2.9 *0.55*	3.4 *0.58*	2.7 *0.55*	2.2 *0.15*	3.0 *0.52*

Treatments

Analysis of Variance between TR × GR and TR × LI showed that defoliation treatments had a highly significant effect ($P<0.001$) on 1st leaf weight. There was no interaction between GR or LI and TR.

Duncans Multiple Range Test was used to compare Treatments. The residual mean square from a second Analysis of Variance on TR × GR, with TR averaged over all LI, provided the estimate of variance.

Treatments fell into two clearly defined groups with respect to 1st Leaf weight. In Treatments II, III and VI, the weight was similar to that of the control (I). Mean weight of these four treatments was 3.7 mg $leaf^{-1}$. Treatments IV and V differed significantly from the other four treatments ($P<0.01$) but not from one another. The mean weight of the 1st leaf in these two treatments was 2.8 mg $leaf^{-1}$. The relative effects of the treatments were still pronounced 3 Leaf Appearance Intervals after defoliation.

The results thus show that removal of the two youngest leaf blades (emerged portions), or more, severely reduced 1st leaf weight in at least the next 3 new leaves produced after defoliation. Other defoliation treatments appear to have had no effect.

The reduction in leaf weight, following severe defoliation only, is in agreement with results reported by BEGG & WRIGHT, 1964; ANSLOW, 1968; SIMONS *et. al.*, 1972; and A. DAVIES, 1974.

Growth Rooms

Mean 1st leaf weight in each Growth Room was calculated from Treatments I, II, III and VI, averaged over all LI (1st and 3rd LI only in 20°C room).

Table 5.3.11 : Dry weight of 2nd Blade, mg.

S.E. in italics.

GR	LI	I	II	III	IV	V	VI
5°C	1st	5.6 *0.42*	** † 3.9 *0.36*	5.9 *0.10*	† 2.9 *0.20*	† 2.8 *0.49*	* 5.6 *0.56*
	2nd	5.2 *0.09*	5.4 *0.32*	5.1 *0.19*	3.8 *0.32*	3.4 *0.15*	5.6 *0.50*
	3rd	5.1 *0.19*	5.5 *0.66*	5.6 *0.50*	4.7 *0.07*	3.9 *0.52*	5.9 *0.44*
10°C	1st	4.5	* † 3.7	** 5.7	† 3.6	† 4.2	5.3
	2nd	6.7	5.8	** 5.4	4.2	3.5	5.5
	3rd	6.6	4.8	5.3	4.0	3.8	4.9
20°C	1st	5.1 *0.64*	† 3.1 *0.41*	** 6.2 *0.64*	** † 2.9 *0.22*	† 2.3 *0.28*	5.5 *0.44*
	2nd	3.3 *0.85*					
	3rd	4.5 *0.55*	3.9 *0.81*	* 4.5 *0.63*	4.0 *0.15*	2.9 *0.15*	4.6 *0.62*

† blade cut when emerging

* sampled early

** sampled late

Duncans Multiple Range test showed that 1st Leaves were heavier in the 5°C room (4.0 mg $leaf^{-1}$) than in the 20°C room (3.3 mg $leaf^{-1}$), but the differences between the 5°C and 10°C, and between the 10°C and 20°C rooms, were not significant. Mean weight in the 10°C room was 3.6 mg $leaf^{-1}$.

(b) Weight of 2nd Blade (Table 5.3.11)

Leaf Appearance Interval

Treatments II, IV and V at the 1st LI carried 2nd blades that had been cut whilst they were emerging. In the 5°C and 20°C rooms the mean weights of these cut blades were approximately half the mean weight of intact blades. In the 10°C room, cut 2nd blades were somewhat heavier than expected.

Mean weights and lengths of blades that were cut whilst they were emerging were expected to be one half those of uncut blades at the 1st LI. Thus in a population of tillers, 1st leaves would have ranged uniformly from leaves whose tip was just appearing, to those which had almost fully emerged. The mean length of leaf removed would therefore have been equal to the top half of the blade.

There was no consistent change in 2nd Blade weight during the course of the experiment in the 5°C or 10°C rooms (Treatments I, III and VI). In the 20°C room, 2nd Blades in Treatments I, III and VI tended to be heavier at the 1st LI (5.6 ± *0.34* mg) than at the 3rd (4.5 ± *0.30* mg). The difference was not significant.

Treatments

Leaf blades produced after defoliation reached the 2nd Leaf position in the 2nd and 3rd Leaf Appearance Intervals. The weights of these blades were lower in Treatments IV and V relative to Treatments I (the control), II, III and VI. The lower weights of 2nd Blades in Treatments IV and V correspond to their reduced weights 1 Leaf Appearance Interval earlier when they were in the 1st Leaf position.

Other Defoliation Treatments had no consistent effect on the 2nd Blade weight of leaves produced after defoliation.

Growth Rooms

The mean weight of the 2nd Blade in each Growth Room was calculated using measurements from intact leaves, i.e. from Treatments I, III and VI, 1st and 3rd LI, plus Treatment II, 3rd LI.

5°C	10°C	20°C
5.6 ± *0.15*	5.3 ± *0.26*	4.9 ± *0.26*
(n = 21)	(n = 7)	(n = 21)

The results suggest a tendency for 2nd Blade weight to be lower at higher temperatures. However, the differences between Growth Rooms could not be tested since both TR and LI interacted with GR and an acceptable estimate of variance could not be obtained.

(c) Weight of 3rd Blade (Table 5.3.12)

Leaf Appearance Interval and Treatments

The 3rd Blade was generally absent in Treatments III, IV and V at the 1st LI as a result of defoliation. The weight per blade at the 1st LI was thus very small in Treatments IV and V, as

Table 5.3.12 : Dry weight of 3rd Blade, mg.

S.E. in italics.

GR	LI	I	II	III	IV	V	VI
			**	††	††	††	*
5°C	1st	4.1 *0.50*	3.5 *0.38* †	1.6 *0.27*	0.5 *0.15* †	0.4 *0.06* †	3.9 *0.39*
	2nd	3.9 *0.32*	2.7 *0.26*	4.1 *0.41*	2.0 *0.12*	1.8 *0.12*	4.4 *0.32*
	3rd	3.9 *0.21*	4.0 *0.73*	4.0 *0.48*	3.4 *0.15*	2.5 *0.44*	4.1 *0.35*
			*	** ††	††	††	
10°C	1st	2.5	3.2	1.6	0.7	0.5	2.7
	2nd	4.5	† 2.7	** 5.0	† 2.3	† 2.1	4.5
	3rd	4.8	3.2	3.6	2.5	2.5	3.2
				** ††	** ††	††	
20°C	1st	4.9 *0.52*	4.4 *0.87*	0.3 *0.03*	0.1 *0.03*	0.2 *0.07*	6.0 *0.70*
	2nd	4.3 *0.70*					
	3rd	4.7 *0.59*	4.0 *0.66*	* 3.9 *0.61*	3.3 *0.23*	2.5 *0.19*	4.0 *0.41*

† blade cut when emerging

†† blade cut when "fully" expanded - material consists of some younger and older blades which were not cut, plus some blade stubs.

* sampled early

** sampled late

expected, but it was markedly higher in Treatment III in the 5°C and 10°C rooms. Treatment III was less severe than IV and V because only the 2nd Blade was removed. Treatment IV involved the additional removal of the emerging blade while in Treatment V all blades were removed.

3rd Blades in Treatments III, IV and V showed corresponding differences in blade length at the 1st LI (see section 5.3.7.3). Following removal of the 2nd Blade, there was a consistent trend in all Growth Rooms for the stub to extend further the less severe the defoliation treatment (III < IV < V).

3rd Blades at the 3rd LI had emerged one Interval after defoliation. 3rd Blade weight at the 3rd LI was less in Treatments IV and V than in the other treatments. This reduction corresponds to the lower weights of the same leaves during the 2nd and 1st LI (see 2nd Blade and 1st Leaf).

Growth Rooms

The average weight of the 3rd Blade in each Growth Room was calculated from Treatments I, II, III and VI at the 3rd LI:

5°C	10°C	20°C
4.0 ± *0.21*	3.7 ± *0.38*	3.9 ± *0.25*
(n = 12)	(n = 4)	(n = 12)

There appears to have been no difference in 3rd Blade weight between the three environments.

(d) Weight of 4th Blade (Table 5.3.13)

The 4th Leaf was divided into Blade and Sheath in the 5°C and 20°C rooms. The average weight of the sheath in both rooms was 0.9 mg. 0.9 mg was subtracted from 4th Leaf weight in the 10°C room to estimate the Blade weight.

Weights of the 4th Blade are given for the 3rd LI only, since those at the 1st and 2nd LI emerged during the pre-treatment period. Treatments II, IV and V have been omitted because their 4th Blades were cut whilst emerging three leaf appearance intervals earlier.

Table 5.3.13 : Dry weight of 4th Blade.

S.E. in italics.

GR	LI	I	III	VI	Growth Room mean
5°C	3rd	3.0 *0.21*	3.0 *0.20*	3.0 *0.39*	3.1 *0.18* (n=9)
10°C	3rd	3.4	2.3	2.2	2.6 *0.38* (n=3)
20°C	3rd	4.0 *0.21*	4.4 *0.66*	3.7 *0.26*	4.0 *0.24* (n=9)

The results of a t-test suggest that 4th Blade weight was less in the 5°C room than in the 20°C room. There were too few observations to carry out a more reliable analysis.

5.3.7.2 % WATER CONTENT OF 1ST LEAF, 2ND BLADE, 3RD BLADE, 4TH LEAF, AND OLDER MATERIAL

The % water content of fresh leaf material was calculated from:

$$\text{\% water content} = \frac{\text{fresh weight - dry weight}}{\text{fresh weight}} \times 100$$

"Fresh" weight was determined after the tillers had been separated into their component parts. All the plant material was subjected to handling because leaves were peeled away from the central emerging leaf, rather than cut off the tiller. It is unlikely that there was any surface moisture left on the leaves by the time they were weighed, two to three hours after harvesting.

Comparison of the measured water contents with those of BAILEY (1973) and WILMAN *et al.* (1976c) indicate that about 10% or more of internal water must also have been lost - at least from the younger leaves - during tiller separation. The amount lost may have varied with the humidity and temperature conditions of the laboratory. The measurements are, therefore, only rough estimates of water content.

The relative differences between leaf positions and between Growth Rooms can be seen in Table 4.3.14 below, in which observations from all TR and LI have been averaged. The number of observations is shown in brackets.

Table 5.3.14 : % water content of freshly separated leaf material.

S.E. given in italics.

	5°C (n = 54)		10°C (n = 25)		20°C (n = 36)	
1st Leaf	69	*0.4*	71	*0.6*	74	*0.4*
2nd Blade	67	*0.4*	68	*0.6*	64	*1.2*
3rd Blade	60	*1.1*	61	*1.1*	43	*2.4*
4th Leaf	27	*1.8*	22	*1.9*	23	*2.0*
Older material	15	*1.2*	15	*1.3*	11	*0.7*

The results show that leaves, or blades, at successive leaf positions had substantially different water contents. In the 20°C room, water content seems to have begun to decline soon after leaf emergence whereas in the 5°C and 10°C rooms it did not change much until the 3rd Leaf position.

The early fall in water content with leaf position in the 20°C room was not accompanied by an early onset of senescence (as measured by leaf colour in section 5.3.5.2, p. 208). Colour change

Table 5.3.15: Lengths of 2nd Blade and 3rd Blade, mm.

S.E.'s are given in italics.

Growth Room	Leaf Appearance Interval	Defoliation Treatment											
		I		II		III		IV		V		VI	
		2B	3B	2B	3B	2B	3B	2B	3B	2B	3B	2B	3B
5°C	1st	95	89	** 65	81	96	27	57	14	53	7	* 98	89
		2	*2*	*4*	*3*	*2*	*4*	*2*	*2*	*2*	*2*	*2*	*3*
	2nd	88	92	90	57	77	69	64	42	57	37	81	96
		2	*2*	*2*	*3*	*2*	*4*	*1*	*2*	*2*	*3*	*2*	*2*
	3rd	82	87	84	92	83	83	70	73	64	61	82	84
		1	*1*	*1*	*2*	*2*	*2*	*1*	*2*	*2*	*2*	*1*	*1*
10°C	1st	89	68	* 75	86	** 92	35	74	16	83	12	101	84
		2	*3*	*4*	*3*	*2*	*6*	*4*	*4*	*3*	*3*	*3*	*4*
	2nd	120	113	105	51	** 93	110	73	55	67	53	97	105
		4	*4*	*4*	*6*	*4*	*4*	*2*	*4*	*3*	*2*	*2*	*4*
	3rd	116	106	86	75	88	79	69	57	68	63	96	85
		3	*4*	*3*	*4*	*3*	*3*	*2*	*4*	*3*	*3*	*3*	*3*
20°C	1st	122	122	72	110	** 121	56	** 73	30	61	4	112	128
		2	*2*	*3*	*4*	*2*	*5*	*3*	*3*	*3*	*1*	*2*	*2*
	2nd	84	112										
		2	*2*										
	3rd	105	101	92	95	* 95	91	95	81	76	64	97	88
		3	*3*	*2*	*2*	*3*	*2*	*3*	*2*	*2*	*2*	*3*	*2*
Cut Leaves													
	1st LI			†			††	†	††	†	††		
	2nd LI				†				†		†		
	3rd LI												

* sampled early

** sampled late

† cut whilst emerging

†† cut when in 2nd Blade position

began at an earlier Leaf Position stage in the 5°C and 10°C rooms relative to the 20°C room. Their water contents, however, remained fairly high until the 4th Leaf Position.

5.3.7.3 LENGTHS OF 2ND AND 3RD BLADES

The lengths of the 2nd and 3rd Blades were measured at the end of each Leaf Appearance Interval. The mean lengths are shown in Table 5.3.15. The 10°C room means are based on 50 observations; those in the 5°C and 20°C rooms are based on 150.

Leaf Appearance Intervals and Treatments

It was expected that the mean length of blades which were cut whilst they were emerging would be one half the length of uncut blades (see p. 222). It was further expected the length of leaves which had been cut when in the 2nd leaf position would be 0. Table 5.3.15 shows that the measured lengths of cut and half-cut leaves tended to be greater than expected. Part of the discrepancy arose out of tillers not being measured exactly 1 Leaf Appearance Interval later. However, the stub length of leaves cut as 2nd Blades increased in reverse order to the severity of defoliation (3B at the 1st LI was longer in Treatment III than in IV than in V in all Growth Rooms). This effect suggests that some blade extension continued into the 2nd Leaf position and that it was sensitive to defoliation stress. Continued blade extension in the 2nd position would also account for the cut emerging blades reaching a greater length than expected.

By the 3rd LI, the 2nd and 3rd Blades were generally very similar in length. The treatments fell into two groups. Blade length in Treatments II, III and VI did not differ from that in the control whereas in Treatments IV and V it was about 25% less. It

therefore appears that leaf expansion was only affected when defoliation was severe (2 or more younger leaves removed). The effect was smaller in the 20°C room.

Growth Rooms

Blade length was shorter in the 5°C room than in the other two growth rooms. Mean Blade length in each Growth Room has been calculated from the 2nd Blades in Treatments I, II, III and IV at the 3rd LI:

5°C	10°C	20°C
83 ± *0.7* mm	96 ± *1.5* mm	97 ± *1.4* mm
(n = 600)	(n = 200)	(n = 550)

Both MITCHELL (1956-7) and COOPER (1964) observed a larger increase in leaf length between 5°C and 13°C than between 10°C and 25°C, as occurred in this experiment. In winter leaves were twice as long in a heated greenhouse than outdoors (ROBSON, 1967); on the other hand, in the warmer temperatures of summer, outdoors, THOMAS (1975) found that the relationship between leaf length and temperature was not a close one. These observations suggest that the increase in length of successive leaves up until mid or late summer (ALBERDA & SIBMA, 1968) is not solely a consequence of the rise in mean temperature.

Rates of blade extension in the different growth rooms have been estimated by dividing 2nd Blade length at the 3rd LI by the length of the 2nd leaf appearance interval:

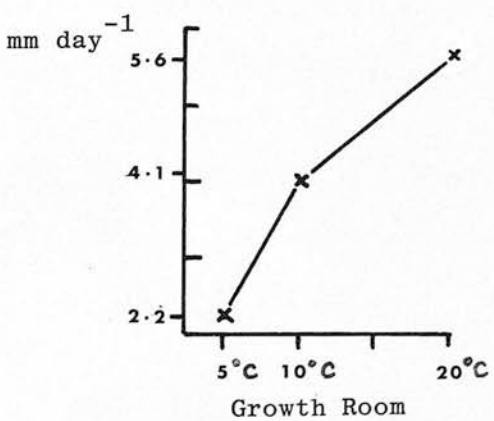


Fig. 5.3.4 : Estimated rate of blade extension

Table 5.3.16 : Dry weight per unit length of 2nd Blade, mg m^{-1} (× 10). *S.E. given in italics.*

GR	LI	I	II	III	IV	V	VI	Interval mean
5°C	1st	592 *29*	588 *24*	615 *8*	498 *35*	503 *61*	568 *41*	561 *17*
	2nd	594 *25*	593 *19*	663 *10*	592 *29*	569 *19*	691 *22*	617 *13*
	3rd	632 *57*	653 *81*	674 *57*	681 *50*	611 *33*	714 *43*	661 *21*
10°C	1st	510	470	614	482	500	526	517 *30*
	2nd	563	564	579	576	519	569	559 *9*
	3rd	569	558	600	571	560	507	561 *12*
20°C	1st	414 *22*	432 *31*	514 *43*	427 *2*	456 *1*	489 *23*	455 *12*
	2nd	386 *88*						
	3rd	483 *1*	412 *59*	475 *23*	422 *11*	381 *18*	465 *20*	437 *14*

5.3.7.4 DRY WEIGHT PER UNIT LENGTH OF BLADE

Weight per unit length expresses herbage weight in a form that may be useful in studies of grazing mechanics: bite size is a variable that affects herbage intake (HODGSON, 1977). Weight per unit length was derived by dividing the mean length of the Blade (section 5.3.7.3) into the mean weight (section 5.3.7.1).

(a) Weight per unit length of 2nd Blade (Table 5.3.16)

Analysis of Variance showed that Growth Rooms and Treatments had significant effects, and that there was an interaction between GR × LI.

Leaf Appearance Intervals

Weight per unit length in the 5°C room increased during the experiment from the 1st LI to the 2nd LI ($P<0.05$); the apparent increase between the 2nd and 3rd LI was not significant. In the 10°C and 20°C rooms, weight per unit length did not alter as the experiment progressed.

Treatments

Treatments were compared using Duncans Multiple Range Test. The estimate of variance was provided by the residual mean square in an Analysis of Variance on GR × TR. As in analyses of other measurements, each GR·TR was averaged over all LI in order to obtain an estimate of variance based on a balanced number of observations.

Treatments fell into the following overlapping groups:

V	IV	II	I	VI	III	
502	519	521	527	554	581	mg m^{-1} (×10) (i.e. mg per 1000 cm)
a	a	a	ab	bc	c	

Treatments with the same subscript in common did not differ significantly in weight. The only Treatment which differs significantly from the control is III (2nd blade removed). The increased weight per unit length compared with other treatments is particularly marked in the 1st LI. Tables 5.3.11 (p. 222) and 5.3.15 (p. 227) show that Treatment III led to an increased weight in the leaf that was emerging when the leaf below was removed, but that there was no effect on its length. There are no noteworthy differences in the 2nd blade weight, length or weight per unit length of Treatment III compared with other Treatments at subsequent LI.

Growth Rooms

Since weight per unit length of the 2nd Blade changed during the experiment in the 5°C room, comparison between Growth Rooms has been made at the 3rd LI only, averaged over all TR.

5°C	10°C	20°C	
661 ± *21*	561 ± *12*	437 ± *14*	mg m^{-1} (× 10)
(n = 18)	(n = 6)	(n = 17)	

Weight per unit length differed considerably between Growth Rooms ($P<0.001$). In the 5°C room there was 18% more weight per unit length of the 2nd blade than there was in the 10°C room, and 51% more than in the 20°C room.

(b) Weight per unit length of 3rd Blade (Table 5.3.17)

Analysis of Variance showed that Treatments and Growth Rooms had significant effects on the 3rd Blade weight-length ratio. There may have been a certain amount of interaction between TR and LI ($P=0.09$).

Table 5.3.17 : Dry weight per unit length of 3rd Blade, mg m^{-1} (× 10). *S.E. given in italics.*

GR	LI	I	II	III	IV	V	VI	Interval mean
5°C	1st	450 *34*	445 *16*	†† 543 *41*	†† 327 *33*	457 *9*	435 *32*	444 *19*
	2nd	415 *18*	† 419 *36*	497 *21*	† 436 *20*	† 443 *11*	466 *36*	446 *11*
	3rd	458 *54*	425 *57*	483 *51*	478 *45*	406 *26*	500 *60*	458 *19*
10°C	1st	369	373	†† 433	†† 404	†† 418	315	385 *17*
	2nd	396	410	454	† 402	† 397	429	415 *9*
	3rd	451	424	453	396	398	373	416 *13*
20°C	1st	401 *14*	394 *51*	†† 455 *64*	†† 362 *25*	583 *53*	471 *23*	436 *22*
	2nd	399 *91*						
	3rd	427 *29*	418 *57*	428 *25*	406 *28*	394 *20*	451 *17*	420 *12*

† blade cut when emerging

†† blade cut when "fully" expanded - material consists of some younger and older blades which were not cut, plus some blade stubs.

Treatments

Treatments were compared as described under Weight per unit length of 2nd Blade:

IV	II	I	VI	V	III	
400	413	418	433	442	463	mg m^{-1} (× 10)
a	ab	ab	ab	ab	b	

Apart from Treatment V, the ranking order is fairly similar to that for the 2nd Blade weight per unit length. This is to be expected since observations on the 2nd and 3rd Blades were made from the same tillers.

Only Treatments III and IV differed significantly from one another ($P<0.05$) so it is concluded that defoliation had little effect on weight per unit length of the 3rd blade.

A number of the weight-length ratios in Table 5.3.17 were based on cut leaf blades (II, IV, V at the 2nd LI) or blade stubs (III, IV, V at the 1st LI). The weight-length ratio of this cut material did not differ consistently from that of uncut blades.

Growth Rooms

Weight per unit length of the 3rd Blade was averaged over all TR × LI:

5°C	10°C	20°C	
449 ± *10*	405 ± *8*	426 ± *12*	mg m^{-1} (× 10)
(n = 53)	(n = 18)	(n = 36)	

Duncans Multiple Range Test, using the same estimate of variance as that used for the Treatment comparisons, showed that weight per unit length of 3rd Blade was greater in the 5°C room than in the 10°C room ($P<0.05$) but that all other comparisons between Growth Rooms were insignificant.

The weights per unit length measured in Experiment 2 were similar to those reported by THOMAS (1975) in swards that had recently been removed from growth rooms. They were rather lower than those which subsequently developed in THOMAS's material after the swards had grown for a few weeks out of doors under higher light intensities ($800\,mg\,m^{-1}$ ($\times 10$)). These results correspond to MITCHELL & SOPER's observation (1958) that leaf blades are narrower and less thick at low light intensities (confounded with higher temperatures in their experiment).

DE LUCIA SILVA (1974) found that weight per unit length was greater in expanding than in mature leaves. However, whereas in this experiment the severity of defoliation had no effect on weight per unit length, in DE LUCIA SILVA's plants there was a tendency for weight per unit length of the mature leaves to be less in those tillers which had been more severely defoliated. This suggests that remobilization may have been stimulated. It is possible that the slow rates of leaf appearance in Experiment 2 led to a low demand for assimilate, and that consequently such remobilization did not occur.

In this experiment, weight per unit length of the 2nd blade fell by about the same amount between 5°C and 10°C as between 10°C and 20°C. Similar differences between temperatures are indicated by MITCHELL's (1956-7) measurements of leaf length and leaf width, but he does not specify which leaves were measured.

5.3.7.5 FACTORS DETERMINING THE WEIGHT OF DRY MATTER ABOVE SOIL LEVEL

(a) TILLER DENSITY (Table 5.3.18)

Tiller numbers on day DD were estimated from Treatment III in the 5°C and 10°C rooms. Results from the 20°C room are not available.

Tiller density did not differ between Blocks (see p. 185). Mean number of tillers per 10 cm^2 was 35 ± *1*.

Tiller counts were carried out again at the 3rd LI on all remaining mini-plots. There were thus 6 counts per treatment in the 5°C room, 4 in the 10°C room, and 3 in the 20°C room. The results are shown in Table 5.3.18.

Table 5.3.18 : Number of tillers per 10 cm^2 at the 3rd LI.

S.E. in italics.

GR \ TR	I	II	III	IV	V	VI
5°C	36.8 *1.1*	30.3 *1.2*	32.4 *1.4*	30.7 *1.1*	33.4 *2.1*	30.9 *1.7*
10°C	30.3 *1.7*	30.7 *0.8*	33.2 *1.3*	33.1 *0.9*	37.1 *1.2*	35.6 *2.8*
20°C	15.0 *3.2*	21.8 *1.9*	23.2 *2.9*	19.2 *1.5*	27.3 *2.6*	26.8 *1.0*

Tiller density was extremely high: densities were two to seven times greater than those found in the field. A very high seeding rate had been used, and cutting followed by fertilizer application during establishment would have further increased tiller numbers.

Leaf Appearance Interval

Tiller densities in the 5°C and 10°C rooms at the 3rd LI were similar to those at DD. No comparison is possible for the 20°C room.

Treatments

Tiller densities tended to be higher in Treatments V and VI in the 10°C and 20°C rooms. Both treatments would have led to a considerable increase in light penetration to the tiller buds at the base of the sward. In Treatment VI all the older blades, and in Treatment V all the older blades plus all the younger blades, were removed. This effect was not, however, observed in the 5°C room. Furthermore, there was little visible evidence in the 10°C and 20°C rooms that much daughter tiller development had taken place.

Growth Rooms

Mean tiller density in each Growth Room was calculated over all TR:

5°C	10°C	20°C
32.3 ± *0.7*	33.6 ± *0.8*	22.2 ± *1.3*
(n = 33)	(n = 21)	(n = 18)

Tiller density was one third lower in the 20°C room than in the 5°C and 10°C rooms ($P<0.01$, Duncans Multiple Range Test). However, there is no evidence to show whether this difference had already arisen by the time the experiment started.

There were more dead tillers (completely brown or 1st Leaf dying) in the 20°C room at the 3rd LI than in the other two rooms.

Table 5.3.19 : Number of dead tillers per 10 cm^2 at the 3rd LI.

S.E. in italics.

GR \ TR	I	II	III	IV	V	VI	GR means
5°C	0.28	0.04	0.00	0.12	0.09	0.12	0.11
	0.14	*0.04*	*0.00*	*0.05*	*0.05*	*0.06*	*0.03*
10°C	0.06	0.12	0.19		0.06	0.19	0.11
	0.06	*0.15*	*0.12*		*0.06*	*0.12*	*0.04*
20°C	9.8	2.04	2.68	2.50	0.74	1.02	2.74
	3.22	*0.94*	*0.97*	*0.97*	*0.09*	*0.09*	*0.75*

From Tables 5.3.18 and 5.3.19, it can be seen that 40% of the tillers in Treatment I, 20°C room, were dead (10 dead tillers to every 15 live tillers per 10 cm). Only 3% of tillers in Treatments V and VI, and 10% in II, III and IV (all at 20°C) were dead. The amount of tiller death in the 20°C room seems to have been related to the penetration of light to the base of the sward.

It has already been pointed out that Treatments V and VI would have greatly increased light penetration. Treatments II (1st blade removed), III (2nd blade removed) and IV (1st and 2nd removed) would not of themselves have led to a large increase in light penetration through the older material, but the handling involved when implementing these treatments might have done.

The differences in tiller number within the 20°C room may also have been partly due to more tiller production under improved light conditions (WILSON & McGUIRE, 1961). It seems unlikely, however, that this occurred since there was little visible evidence of tillering. Moreover, the very large proportion of dead tillers in Treatment I suggests that tiller death was much the most important factor. The reason why a denser base to the sward should appear to be associated with increased tiller death is not clear. The situation may be comparable to that observed by ALBERDA, quoted by A. DAVIES (1977), where there was a 'marked increase in tiller deaths when alternate rows of plants were arranged so that the rows being investigated were overtopped'.

(b) DRY WEIGHT PER TILLER

Leaf weight measurements have already been presented in section 5.3.7.1, p. 220. Weights in each Growth Room are summarised below:

	5°C	10°C	20°C
1st Leaf, mg	4.0	3.6	3.4
2nd Blade, mg	5.6	5.3	4.9
3rd Blade, mg	4.0	3.7	3.9
4th Blade, mg	3.1	2.6	4.0
Total, mg	16.7	15.2	16.2

The weight of older leaves (attached and unattached) plus dead tillers, that was contained in the subsample of 50 tillers used for measuring leaf blade weights, is given below:

Table 5.3.20 : Total dry weight of 5th and older leaves (attached or unattached), plus dead tillers at the 3rd LI. Weight is expressed as mg tiller^{-1}. *S.E. in italics.*

GR \ TR	I	II	III	IV	V	VI	GR means
5°C	4.4	2.4	4.1	1.6	1.0	2.9	2.7 (n=18)
	1.8	*0.3*	*0.9*	*0.4*	*0.3*	*0.3*	*0.5*
10°C	5.3	2.7	1.8	1.2	1.9	2.4	2.5 (n= 6)
	-	-	-	-	-	-	*0.8*
20°C	35.7	13.7	8.4	7.9	8.6	5.2	13.5 (n=17)
	11.8	*2.8*	*1.0*	*1.0*	*5.9*	*0.5*	*4.4*

It is emphasised that the figures quoted in Table 5.3.20 are approximate values. The amount of loose dead material associated with the 50 tillers was only roughly apportioned to the subsample.

There was a much greater weight of older leaves plus dead tillers on a per tiller basis in the 20°C room than in the other two rooms. This was partly due to the large number of dead tillers but it could also have been due to a slower rate of disappearance of dead material per leaf appearance interval.

A slower rate of litter disappearance would partly reflect the shorter length of the leaf appearance interval at 20°C but the 10°C interval was also much shorter than the 5°C interval. Two further factors may have been involved:

(1) the much harder texture of leaves in the 20°C room, which might make them more resistant to microbial attack;

(2) the large temperature range from 19.3°C by day to 4.4°C at night which could perhaps have been unfavourable to growth of organisms which decompose plant tissue.

(c) WEIGHT OF DRY MATTER ABOVE SOIL LEVEL

The yields from all TR × GR × LI samples are listed in Appendix 12. The word 'yield' refers here to the total weight of dry matter above soil level. TR·GR yields, at the 3rd LI only, are presented in Table 5.3.21.

Table 5.3.21 : Weight of dry matter above soil level at the 3rd LI, g m-z. *S.E. in italics.*

GR \ TR	I	II	III	IV	V	VI	GR means
5°C	858	785	876	613	502	(962)	727 *
	90	*50*	*24*	*14*	*30*	*288*	*43*
10°C	787	497	638	442	498	711	595
							56
20°C	658	692	709	476	294	614	574
	86	*39*	*67*	*57*	*44*	*29*	*39*
TR means	768	658	741	510	431	662 **	

* Mean of Treatments I to V in the 5°C room

** Mean of 10°C and 20°C rooms only

By the 3rd LI, leaves 1 to 3 in all Treatments had appeared since defoliation. The 4th Leaf in Treatments II, IV and V had been partially defoliated whilst emerging.

Treatments

Analysis of Variance between TR × GR at the 3rd LI showed that Treatments had a significant effect on dry matter yield ($P<0.01$). Duncans Multiple Range Test was used to compare Treatments. Treatments fell into two groups corresponding to the severity of the defoliation treatment. Treatments IV and V produced a lower yield than in the other treatments. The reduction in Treatment V was more marked (39%; $P<0.01$) than in Treatment IV (28%; $P<0.05$) but IV and V did not differ significantly from one another.

Growth Rooms

Dry weight per unit area of ground was greater in the 5°C room than in the other two environments at the 3rd LI ($P<0.01$, Duncans Multiple Range Test). If the very extreme measurement made in TR VI at 5°C is omitted, the difference is still significant ($P<0.05$).

The heavier weight of dry matter per unit area of ground in the 5°C room (at the 3rd LI) relative to the 10°C room appears to be associated with the heavier weight of the first 4 leaves (p. 235) since there was no difference in tiller numbers (Table 5.3.18) or weight of older material (Table 5.3.20). The difference in leaf weight is, however, not sufficient to account for the difference in yield (9% lower leaf weight, 18% lower yield). The difference must have been due to sampling error or some difference in sheath weight.

Lower yield in the 20°C room relative to the 5°C appears to have been related to a lower tiller density and lower weights of the youngest 3 leaves. Tiller density in the 20°C room was 67% of that in the 5°C room. The lower tiller density was, to some extent, counterbalanced by an increased weight of older leaves and the large number of dead tillers.

Chapter Six

Definitions of expressions used in Chapter Six

Leaf appearance interval — Number of days between the appearance of successive leaves on a tiller.

SLI (see p. 244) — Leaf position on a tiller in terms of the number of whole (e.g. 2) and incomplete (e.g. 0.2) leaf appearance intervals since its emergence.

SLI_{max} — The oldest position at which leaves are found on a tiller. In practice, SLI_{max} is determined by the oldest position at which measurements have been made of leaf size and digestibility.

W(SLI) (see p. 248) — function relating Weight of a leaf (in mg) to its position on the tiller (in SLI units).

$W_E(SLI)$ — as above, but specifically for established vegetative tillers (E);

$W_D(SLI)$ — ditto, but for daughter tillers (D);

$W_R(SLI)$ — ditto, but for reproductive tillers (R);

$W_R(SLI)_{blade}$ — ditto, but for leaf blades only, on reproductive tillers;

$W_R(SLI)_{sheath}$ — ditto, but for leaf sheaths only, on reproductive tillers;

$W_R(SLI)_{stem}$ — ditto, but for stem plus inflorescence only, on reproductive tillers.

P(SLI) (see p. 248) — Function stating the percentage of tillers in the population that are carrying a leaf at a particular position on the tiller; the position is described in SLI units.

N	Number of tillers per unit area of ground, e.g. per m^2.
N_E	as above, but specifically established vegetative tillers.
N_D	ditto, but daughter tillers;
N_R	ditto, but reproductive tillers;
$N_{R,head}$	Number of reproductive tillers, per unit area, in which the stem has started elongating so that the heads are elevated above ground level.
$G_E(SLI)$ (see p. 264)	Function relating the rate of weight change in a leaf (vegetative tillers) (in mg day^{-1}) to its position on the tiller (in SLI units);
$G_R(SLI)_{stem}$	Function relating the rate of weight change in the stem internodes and inflorescence (reproductive tillers) to their age in SLI units.
$D(SLI)$ (see p. 269)	Function relating the percentage (by weight) of tissue removed by defoliation, to the age of the leaf or stem (in SLI units). The form of this function is determined by the grazing mechanics compartment of a larger model.

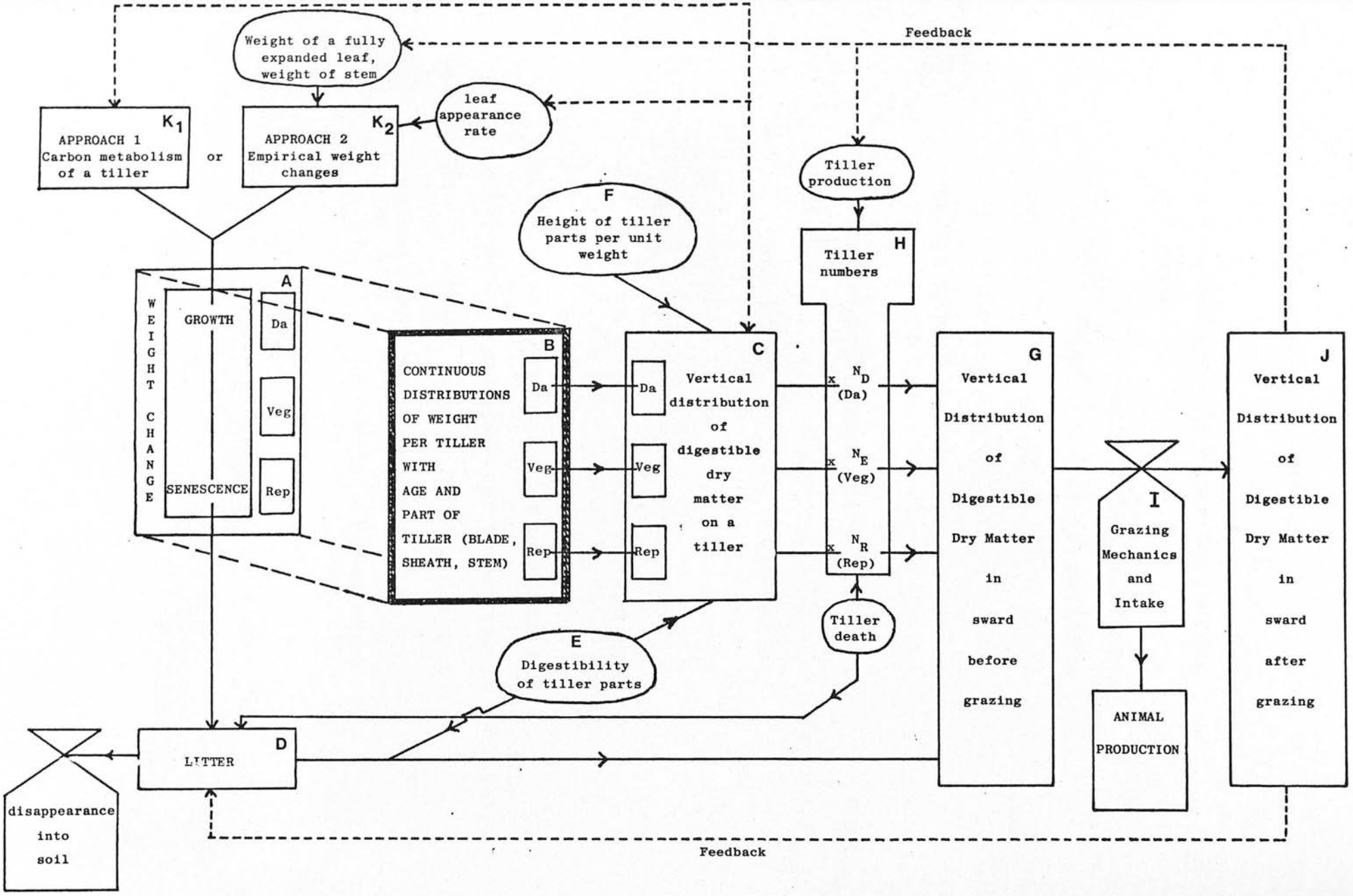


Fig. 6.1 : Structure of the pasture model.

Full lines represent direct links between the compartments; dotted lines indicate feedback effects.

Da = daughter tillers; Veg = established vegetative tillers; Rep = reproductive tillers.

CHAPTER SIX

FORMULATION OF A PASTURE MODEL FOR GRAZING STUDIES

INTRODUCTION

The discussion will outline a general approach to the synthesis of a pasture model for grazing studies. Information from the 1st and 2nd Experiments, and the literature, will be used to make quantitative statements about the components in the model.

The objectives that should be met by a pasture model for grazing studies have been outlined, *viz*:

(1) Pasture should be represented in a form to which the mechanics of grazing can be applied;

(2) The effect of grazing should feed back into pasture structure and growth;

(3) Herbage growth should be modelled in sufficient detail to allow the model to be operated under a wide range of environmental and management conditions.

To meet these objectives, the model has been organised in the form shown by Fig. 6.1. The tiller forms the basic unit of the model. In compartment A, weight changes due to the processes of growth and senescence are used to update the distribution of weight within different parts of the tiller (compartment B). The structure of the tiller is described by the weight of leaves, stem (compartment B) and associated litter (compartment D); the digestibilities of these parts (compartment E); and their heights (compartment F). The structure of the sward (compartment G) is derived from the structure of vegetative, reproductive and daughter tillers (compartment C) according to their relative numbers (compartment H).

Material is harvested from the sward structure according to the mechanics of grazing and factors controlling intake (compartment I). The sward components left behind (compartment J) affect the production of new herbage (compartments K_1 or K_2, and H), and litter (D).

It has been shown in the Literature Review that the requirements of a grazing model can be met by using the tiller as the basic unit of dry matter production and pasture structure (p. 90). The intake of an animal at pasture is, to a large extent, a function of the digestibility of the herbage it ingests, and of the 'availability' of the herbage. Availability is defined in the context of this discussion as the weight of dry matter on offer, as it is influenced by the relative spatial distribution of the component parts of that dry matter.

The component parts of the sward can differ substantially in nutritive value (review section 3.2.4), and the structure of a tiller is such that these parts are not distributed at random within the sward. Animals tend to graze the sward progressively in layers from the top of the sward downwards, and may actively select within or between layers (section 3.3.2). The digestibility of, and the amount of herbage eaten by, the animal are thus likely to be much influenced by the structure of the sward.

The response of the pasture to defoliation by grazing is mediated through its effect on the carbon economy of the plant. The leaf area remaining and its photosynthetic capacity, the amount of mobilizable energy in the stubble, the use of current and stored assimilate in maintenance respiration, the partition of the remaining assimilate between sinks, and the loss of old tissue, all affect the rate at which pasture grows after defoliation (section 3.3.3).

Grass growth takes place at the level of the tiller through the continual production of new leaves, new tillers and, at certain times of the year, the development of the reproductive stem (section 3.1).

A basic step in constructing the model is, then, to develop a method for representing the tiller.

Preliminary considerations of the requirements of a pasture model (Chapter 2) suggest that 'leaf-position' boxes could be used to represent the structure of the sward as it is presented to the grazing animal. The first 'box' would represent the emerging leaf. The second box the first fully-expanded leaf, the third box the second fully-expanded leaf, and so on. Growth would be simulated by the addition of new material into the 1st box; leaf maturation and senescence would be represented by moving an amount of material from one leaf position box down to the next. The rates at which material was to be added and subtracted to the tiller would be determined by the rate of leaf appearance, each successive leaf on the tiller moving down one position when a new leaf appeared. The material in a leaf position box would be further described by the mean horizon in which it lay, and by its mean digestibility.

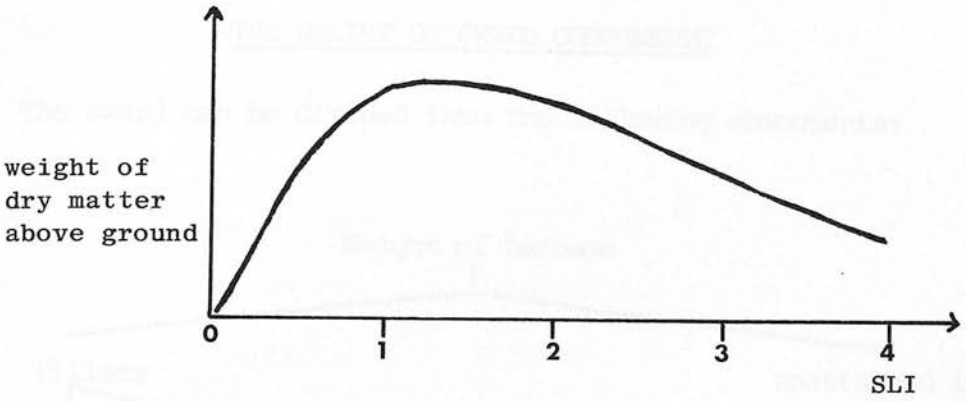
The results of Experiments 1 and 2 suggest, however, that this preliminary concept for representing the pasture should be modified. The results show that large changes in digestibility take place as leaves age from one 'leaf position' to the next. If leaf position were to be regarded as a continuous variable rather than a discrete one, then changes in weight, digestibility and height could be more sensitively represented. As a result, the digestibility of material

eaten by the animal may be more closely monitored; this in turn will allow the model to examine in greater detail the sward factors which influence animal intake.

Representation of the pasture as a continuous distribution of leaf weight in relation to leaf position on the tiller (expressed in leaf appearance intervals).

The position of a leaf on a tiller can be described in terms of the number of leaf appearance intervals that have elapsed since it made its first appearance. A leaf whose tip is just emerging is 0 leaf appearance intervals in age; when it is almost fully expanded and the tip of the next leaf is just appearing, it is 1 leaf appearance interval old; when it is half-way between the 2nd leaf position and the 3rd it is 1.5 intervals old; and so on. The term 'Standard Leaf appearance Interval' (SLI) will be used here to describe the age of a leaf in terms of its position on the tiller. The units in which it is measured are position units, not days. The passage of one Standard Leaf appearance Interval (in position units) corresponds to the lapse of time (in days) between the appearance of two successive leaves on a tiller. The 'leaf appearance interval' is used, as before, to refer to the actual length of time between successive leaf appearances, as measured in days.

It is proposed to represent the amount of herbage in a pasture as a distribution of dry matter weight against age in Standard Leaf appearance Intervals:



The distribution of dry matter against SLI provides a common basis for representing the growth of pasture, its structure, and the removal of material from it. Thus, in general, it has been shown that:

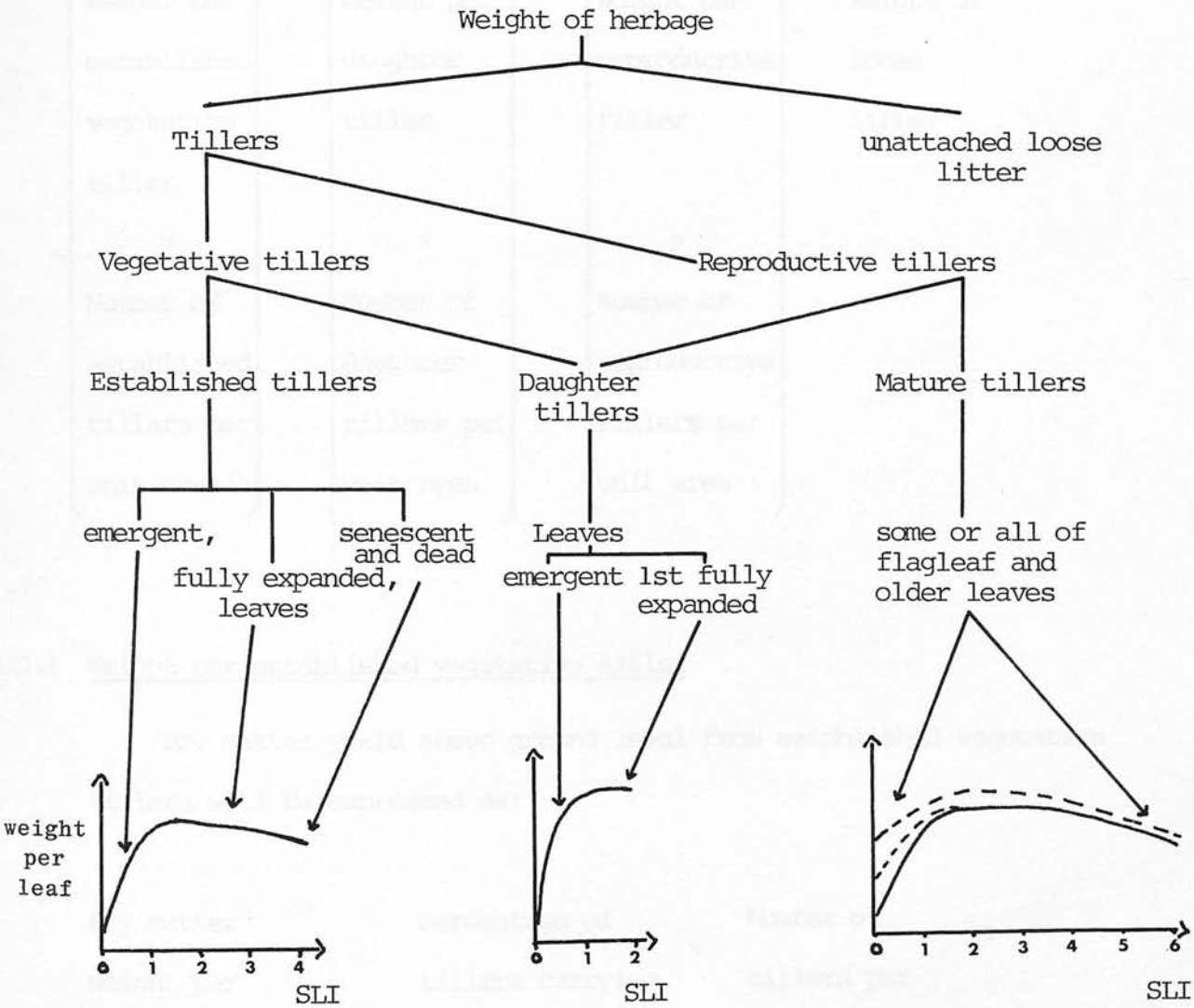
(1) Gross and net growth of a tiller can be understood in terms of the sequence of development that an individual leaf passes through as it ages. These processes could be modelled on an SLI scale. Gross and net growth of pasture could be modelled by combining tiller growth with tiller production and loss; modifications could be introduced to represent development of reproductive tillers.

(2) Defoliation by animals can be examined in terms of the removal or partial removal of parts of the plant. At any point in time, the amount of material within one SLI represents the weight of a particular plant part. Functions could be developed describing the height and digestibility of plant material on the same SLI scale, so that at any point in time the weight, height, and digestibility of the plant parts will be known.

(3) This being so, animals could be made to remove material from the weight distribution according to specified selection rules. Large changes in digestibility, height and weight of plant tissue would be represented on a continuous scale, so allowing more realistic simulation of animal intake from pasture than is possible using the model initially proposed in Chapter 2.

6.2. THE WEIGHT OF SWARD COMPONENTS

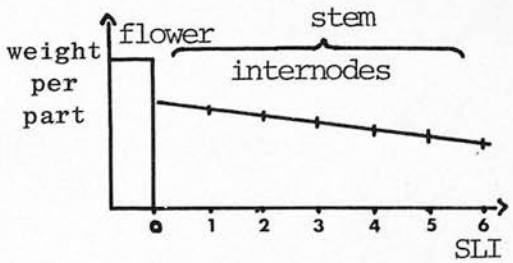
The sward can be divided into the following components:



see p. 248

see p. 254

plus



see p. 255

The total weight of herbage per unit area of pasture at a particular time is equal to:

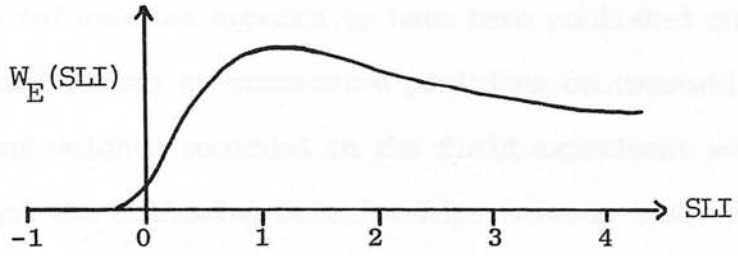
$$\left[\begin{array}{l}\text{Weight per}\\ \text{established}\\ \text{vegetative}\\ \text{tiller}\\ \times\\ \text{Number of}\\ \text{established}\\ \text{tillers per}\\ \text{unit area}\end{array}\right] + \left[\begin{array}{l}\text{Weight per}\\ \text{daughter}\\ \text{tiller}\\ \times\\ \text{Number of}\\ \text{daughter}\\ \text{tillers per}\\ \text{unit area}\end{array}\right] + \left[\begin{array}{l}\text{Weight per}\\ \text{reproductive}\\ \text{tiller}\\ \times\\ \text{Number of}\\ \text{reproductive}\\ \text{tillers per}\\ \text{unit area}\end{array}\right] + \begin{array}{l}\text{Weight of}\\ \text{loose}\\ \text{litter}\end{array}$$

6.2.1 Weight per established vegetative tiller

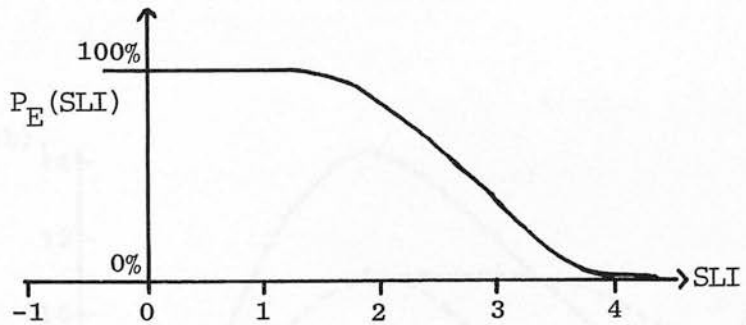
Dry matter yield above ground level from established vegetative tillers will be expressed as:

$$\begin{array}{l}\text{Dry matter}\\ \text{weight per}\\ \text{leaf position}\\ \text{per tiller}\end{array} \times \begin{array}{l}\text{Percentage of}\\ \text{tillers carrying}\\ \text{leaves at each}\\ \text{position}\end{array} \times \begin{array}{l}\text{Number of}\\ \text{tillers per}\\ \text{unit area .}\end{array}$$

Where Dry Matter Weight (W_E) per leaf position (SLI) takes the form:



and the percentage (P_E) of the tillers carrying leaves at each position is given by:



so that, if N_E = number of established tillers per unit area, then

Total dry weight of established tillers per unit area of pasture $= \left[\int_0^{SLI_{max}} W_E(SLI) \cdot P_E(SLI) \right] \times N_E$

SLI_{max} could be set at 6 or 7, i.e. rather more leaves per tiller than is found in practice.

Distribution of leaf weight with leaf position on established vegetative tillers : $W_E(SLI)$

No information appears to have been published on the weights of individual leaves at successive positions on vegetative tillers.

Leaf weights recorded in the field experiment were used to construct the following relationships between leaf weight and leaf position for vegetative tillers of S24 ryegrass at different times of the year. The weights are those of tillers growing under the lowest nitrogen treatment (N1). Leaf weight at SLI = 0 has been set at 10% of mature blade weight (SILSBURY, 1970).

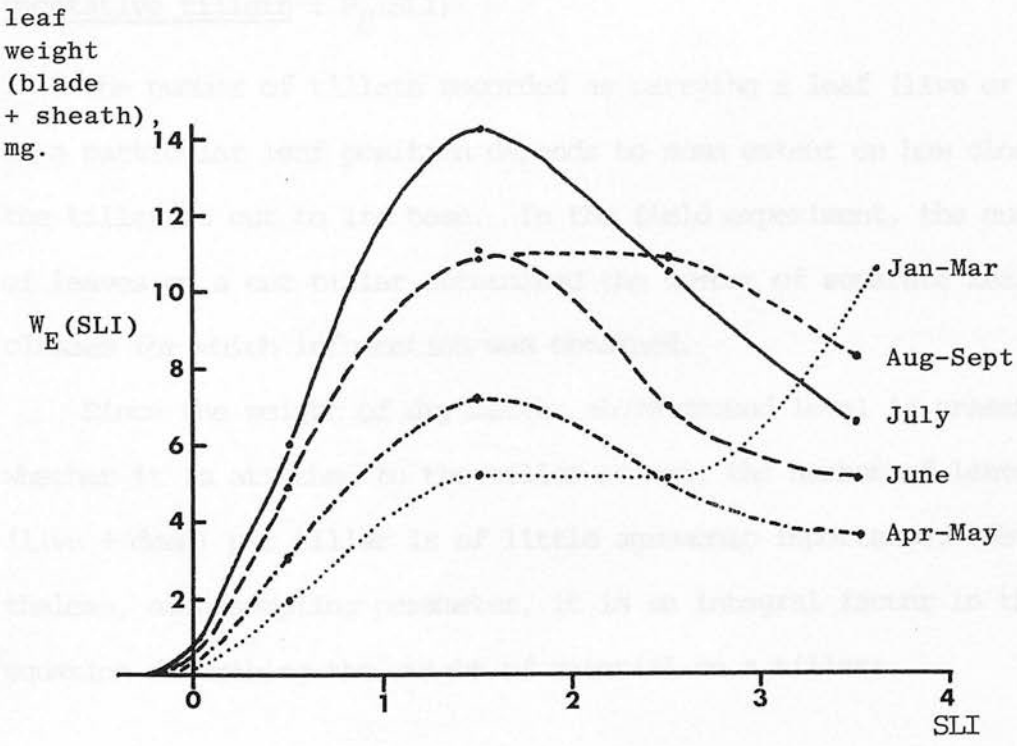


Fig. 6.2

Each line in Fig. 6.2 represents the weights of leaves at different leaf positions on the tiller at a given point in time; it does not portray the course of weight change of an individual leaf.

The weights recorded in the field in May and June were a little lower than those found by A. DAVIES (unpublished) during the same months in Aberystwyth (Appendix 13). Part of the weight difference may have been due to the more severe climate in Edinburgh. The lower weights in Edinburgh may also have been brought about by a mid-May sward cut. Some of the weight difference, however, merely reflects the larger initial weights of the tillers in Aberystwyth; these tillers had previously been grown in a greenhouse.

Percentage of tillers carrying leaves at each position on established vegetative tillers : $P_E(SLI)$

The number of tillers recorded as carrying a leaf (live or dead) at a particular leaf position depends to some extent on how closely the tiller is cut to its base. In the field experiment, the number of leaves on a cut tiller determined the number of separate leaf age classes for which information was obtained.

Since the weight of dry matter above ground level is present whether it is attached to the tiller or not, the number of leaves (live + dead) per tiller is of little agronomic importance. Nevertheless, as a sampling parameter, it is an integral factor in the equation describing the weight of material on a tiller:

$$\text{weight per established vegetative tiller} = \int_0^{SLI_{max}} W_E(SLI) \cdot P_E(SLI)$$

where $P_E(SLI)$ is the proportion of tillers carrying leaves at each SLI position.

The results presented in Table 4.3.9, p. 165, show the percentage of vegetative tillers carrying 1, 2, 3, 4 and 5 leaves. These results were obtained from both established and daughter tillers. If it is assumed that 1- and 2-leaved tillers were daughter tillers, then the following distributions for P_E(SLI) can be obtained:

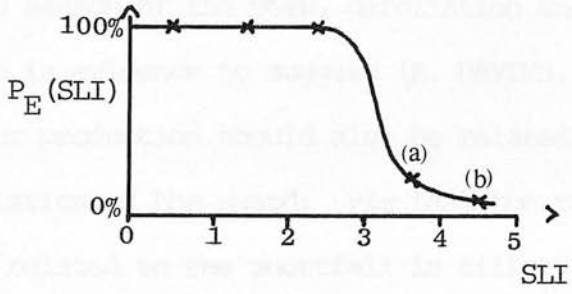


Fig. 6.3

where (a) and (b) take the following values:

Sampling date	(a) % of tillers with 4 leaves	(b) % of tillers with 5 leaves	days since sward last cut
24. 6.74	5.4	0.0	26
2.10.74	17.2	0.0	39
14. 8.74	23.2	0.8	44
4. 5.75	31.6	8.1	over winter
4. 4.75	52.1	22.0	" "
3. 7.75	53.0	13.0	46

In the field experiment, 5th leaves were combined with the litter for digestibility analysis since their number and therefore their weight provided insufficient material. With information on the digestibility of only the first four leaves, plus the combined litter layer, the distribution of P_E(SLI) in the model would be set equal to 0 at SLI $\geqslant$ 4.

Number of established tillers per unit area: N_E

Tiller density has not been considered in detail in this thesis since it was beyond the scope of the observations made in the experiment reported. However, it is apparent from the discussion that a pasture model must include tiller density and tiller population changes. Tiller production and death would both be broadly related to season of the year, defoliation and fertilizer application.

There is evidence to suggest (A. DAVIES, 1977, and unpublished) that tiller production should also be related to the light penetration characteristics of the sward; *viz* that the rate of tillering will be inversely related to the shortfall in tillers present, compared with the maximum tiller numbers that have been observed at a particular time of year. Other factors affecting light penetration will be defoliation and possibly tiller size as affected by fertilizer application.

DAVIES (personal communication) further suggests that tiller death might be modelled as a stochastic process, related to light penetration and to total soluble carbohydrate levels following defoliation.

5.2.2 Weight per daughter tiller

Daughter tillers range widely in size from those which have just appeared through the sheath, or have developed from exposed tiller buds, to those which have grown considerably in size.

Weights and counts of daughter tillers, both enclosed and emerged, are being recorded by BRERETON at Johnston Castle, An Foras Talúntais, Ireland, as part of his pasture studies with S24 ryegrass (personal communication). After weighing the tillers, BRERETON groups the

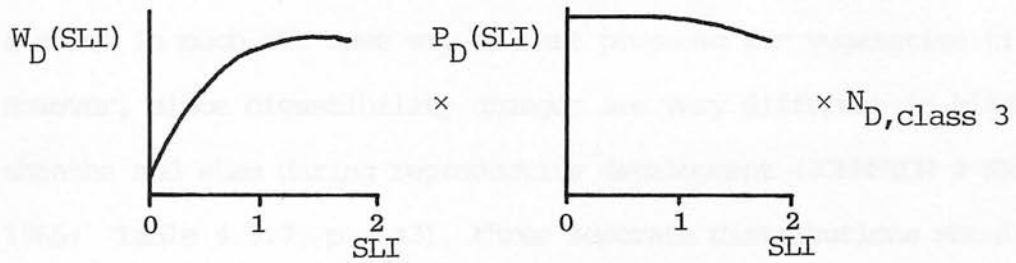
tillers into weight classes which are defined in steps of 25 mg fresh weight, before he carries out further measurements.

It is suggested that a similar system of classification be adopted in the pasture model. Daughter tillers could be classified into three groups on a progressive scale and only the weight distribution of the largest class (largest by size, not tiller number) need be taken into account. The dimensions of tillers in the groups at the smaller end of the scale would generally render them too small to be grazed. However, a tally of their production and survival would have to be kept since they form the reservoir for future 'established tillers'.

Number of daughter tillers

A. DAVIES (1974) has demonstrated that, for every leaf appearance interval, 0.62 daughter tillers can, in theory, be produced. The assumption is made that every tiller bud in the axil of a 2nd fully emerged leaf develops into a tiller. In the model, the percentage of tiller buds actually developing into tiller class 1 (e.g. 0 to 1.0 mg) could be constrained by functions relating bud development to season, fertilizer status, sward defoliation, sward density and apical dominance by reproductive tillers (LANGER, 1974). Presumably tillers in class 1 either die or develop into class 2 tillers (e.g. 1.0 to 4.0 mg), which in their turn die or progress to class 3 (e.g. 4.0 to 10.0 mg) and thence into the 'established tiller' pool.

Great flushes in tiller production can occur, such as those reported in June and September 1974 (p. 165) in Experiment 1. In such circumstances, where 1- and 2-leaved tillers made up 33% of the sward, it would be essential to be able to represent the leaf weight distribution for daughter tillers. If the weight of class 3 tillers only is taken into account, then <u>weight per daughter tiller</u> can, in theory, be represented in the same manner as for established tillers but using only two SLI leaf positions:



RYLE & POWELL (1972) found that rootless daughter tillers of *Lolium multiflorum* generally only carried one or two expanding leaves. If it is assumed, as on p. 251, that the 1- and 2-leaved tillers recorded in the field experiment (Table 4.3.9) were daughter tillers, then the following distributions for P_D(SLI) are obtained:

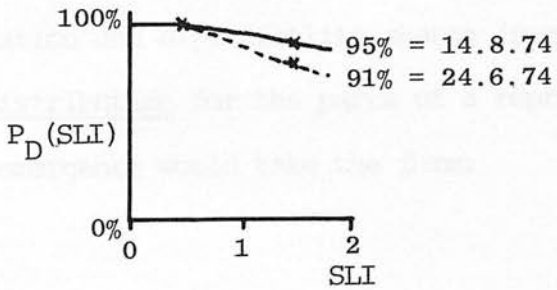


Fig. 6.4 : Percentage of tillers carrying leaves at each position on class 3 daughter tillers (from Expt. 1)

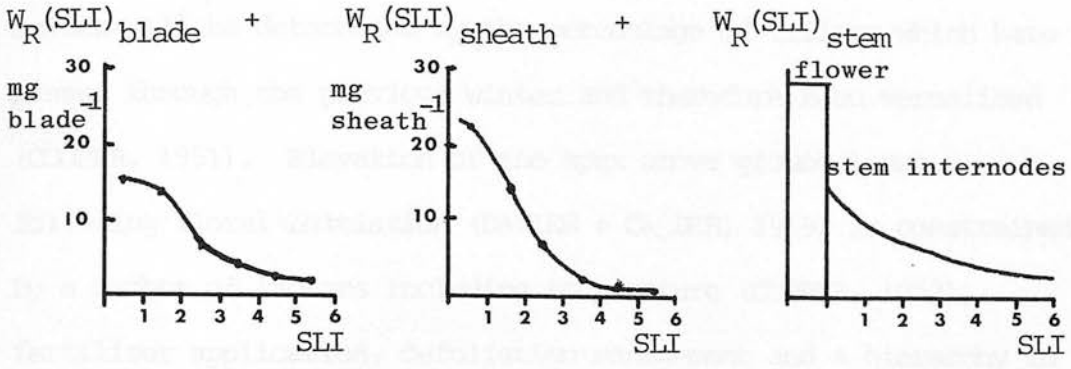
The weight, height and digestibility results of Experiment 1 make no distinction between daughter and established tillers. A height distribution would be necessary for class 3 daughter tillers in addition to the weight distribution, but a digestibility distribution with leaf position appears superfluous where only 2 young leaves per tiller are involved (see p. 138).

6.2.3 Weight per reproductive tiller

The dry weight of reproductive tillers can be represented in a model in much the same way as that proposed for vegetative tillers. However, since digestibility changes are very different in blades, sheaths and stem during reproductive development (JOHNSTON & WAITE, 1965; Table 4.3.7, p. 143), three separate distributions should be used to represent the dry weight on a reproductive tiller - one for the leaf blades, one for the sheaths, and one for the flowering stem.

The weight distribution for stem and flowering head should be divided into internodes plus head in the same way that the vegetative tiller is divided into leaf positions on a standard leaf appearance interval scale. It is necessary to distinguish between different parts of the stem because basal and upper internodes follow different patterns of maturation and digestibility change (see Lit. Rev. p. 60).

The weight distribution for the parts of a reproductive tiller, $W_R(SLI)$, at head emergence would take the form:

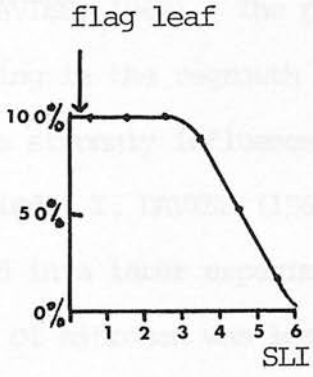


leaf blades (expt. 1, May 26th: 50% ear emergence)

leaf sheaths (expt. 1, May 26th)

stem (notional. In expt. 1, flower = 23.6 mg and total stem = 57.8 mg on May 26th)

while the percentage of tillers carrying leaves at each leaf position would be:



(Expt. 1, May 26th)

The number of head-bearing tillers, $N_{R,head}$, in the sward at any one time depends on (1) the percentage of tillers that have formed reproductive apices (N_R), and (2) the proportion of these apices that have been raised above ground level by stem elongation (I. DAVIES, 1969). The percentage of tillers that have formed reproductive

apices will be determined by the percentage of tillers which have passed through the previous winter and therefore been vernalised (COOPER, 1951). Elevation of the apex above ground level, following floral initiation (DAVIES & CALDER, 1969) is constrained by a number of factors including temperature (COOPER, 1952), fertilizer application, defoliation management and a hierarchy in the dominance of some tillers over others (I. DAVIES, 1969).

It was shown in the field experiment that, in uncut swards, 43% of the tiller population produced flowering heads. A range of 33 to 50% is reported by A. DAVIES (1977).

The dominance of some reproductive apices over others is exemplified by the development of secondary reproductive tillers after primary growth reproductive tillers have been removed in a sward cut (I. DAVIES, 1969). The percentage of reproductive tillers developing in the regrowth was found in the field experiment to be strongly influenced by the amount of nitrogen fertilizer applied. I. DAVIES (1969) observed a similar effect of nitrogen, and in a later experiment (I. DAVIES, 1973), deduced that a shortage of nitrogen was leading to a greatly reduced number of head-bearing tillers in certain of his regrowths.

The following balance sheet suggests that the effect of nitrogen fertilizer on the percentage of reproductive tillers in pasture regrowth is a very important component of the response in yield to nitrogen.

Table 6.1 : Regrowth yield on 3rd July, 1975, from plots cut to 4 cm on May 16th. Results from Experiment 1.

	N1	N2	N4
Yield, Kg ha^{-1}	2716 ±124	6022 ±164	7751 ±164
Tillers, m^{-2}*	approx 6000	-	12000
Weight of a vegetative tiller, including litter, mg.	37.5 ±1.7	37.9 ±2.8	32.3 ±4.1
	no significant difference		
Percentage of reproductive tillers in the sward	8%	16-19%	28%
Weight of a reproductive tiller, mg	-	-	146.0

It can be calculated that :-

% yield increase N1 to N4 = 185%

% tiller number increase N1 to N4 = 100%

% vegetative tiller weight increase N1 to N4 = 0%

* Tiller numbers were estimated by dividing yield by mean tiller weight. Mean tiller weight = [(% reproductive tillers × wt. of a reproductive tiller) + (% vegetative tillers × wt. of a vegetative tiller)]. It was assumed that the weight of a reproductive tiller in N1 was the same as that in N4; this is likely to be an overestimate.

Therefore nearly one half (46%) of the 185% yield increase on this occasion must have been due to the presence of 20% more reproductive tillers in the high nitrogen treatment. The substantial increase in yield brought about by 28%, rather than 8%, of reproductive tillers in the sward, may be understood in terms of their greater growth rates and weights.

6.3 PRODUCTION OF NEW MATERIAL AND WEIGHT CHANGE WITH LEAF POSITION

Given an initial distribution of dry matter weight per leaf position, W(SLI), subsequent dry matter production could be modelled at one of two levels:

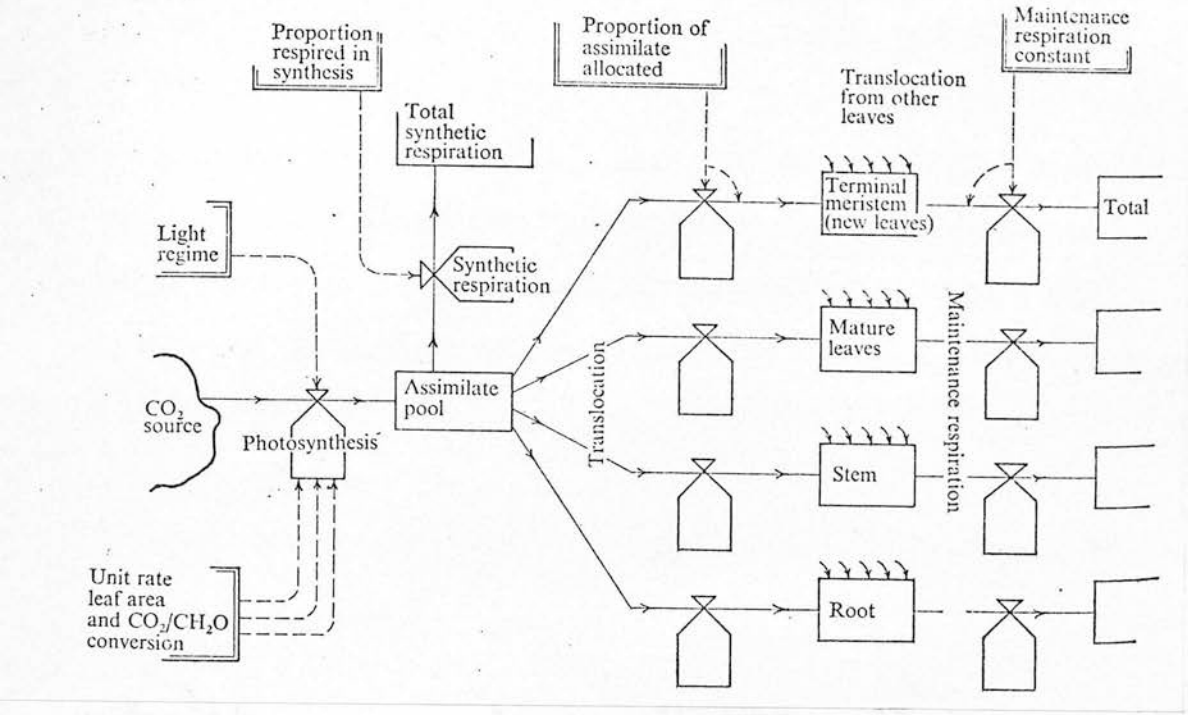
APPROACH (1) The carbon metabolism of the tiller, i.e. assimilate production, respiration, partition, and loss through detachment of old leaves.

APPROACH (2) Empirical weight changes within the tiller.

The first approach is necessary if the plant's response to grazing is to be examined. The second approach is adequate for studies into animal intake as influenced by pasture structure. The information gained from Experiments 1 and 2 will be used to develop an empirical model of pasture weight changes and structure. However, before doing so, it will be shown that the form proposed for representing herbage dry weight (W(SLI)) is one which could be driven by assimilate production and utilization, given the expertise and sufficient data.

6.3.1 APPROACH (1) The carbon metabolism of the tiller

RYLE, BROCKINGTON, POWELL & CROSS (1973) have formulated a computer model for the carbon metabolism and consequent weight changes taking place in the organs of the single-axis barley plant. Their flow diagram for the assimilate produced at one leaf position (e.g. 1L, 2B, 3B, etc.) is shown over the page:-



RYLE *et al.* (1973) used a series of these leaf position units, operating in parallel. The photosynthetic capacity of each leaf varied with its position on the tiller and with its leaf area. 'Synthetic respiration' and the translocation pattern from each leaf unit also varied with position on the tiller. Leaf turnover was simulated by the addition of a new leaf unit at the youngest end of the series, and the simultaneous removal of the oldest leaf unit.

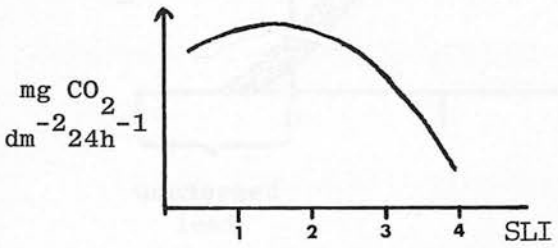
The form of this model could be used for reproductive tillers in S24 ryegrass, given the addition of a fifth sink for axillary tillers and adequate information on the carbon flows. The same model could be modified to simulate carbon flow in vegetative tillers if the stem sink were replaced by one or more axillary-tiller sinks. The mature leaves sink could also be omitted since it receives so little translocated assimilate (RYLE, 1970b). Carbon assimilation

and utilization has been measured in both vegetative and reproductive tillers of S24 ryegrass by RYLE (1970a) and RYLE & POWELL (1974).

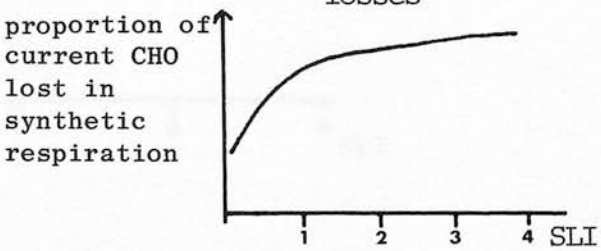
It is desirable in a grazing model to represent leaf position as a continuous variable (see p. 243). RYLE *et al.*'s model, however, is built in discrete leaf position units but the measurements made on carbon processes at successive leaf positions (e.g. RYLE & POWELL, 1974) could be amalgamated into continuous functions of leaf position, i.e. functions of SLI.

For example:

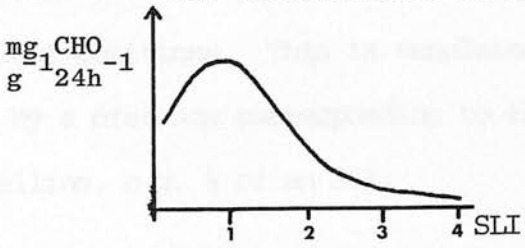
(a) Assimilation rate less



(b) Synthetic respiration losses

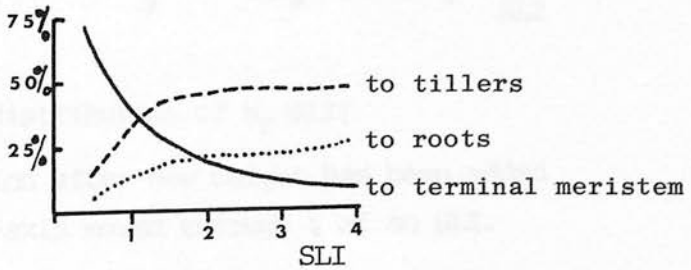


(c) Amount of current assimilate available for translocation to sinks

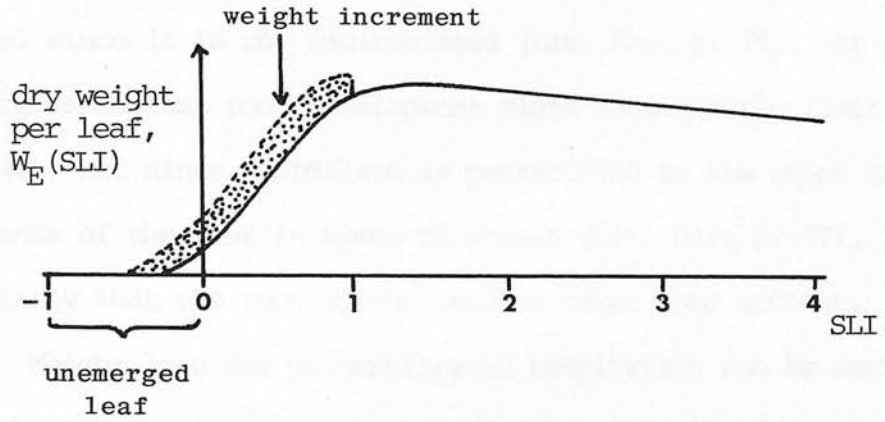


This amount of assimilate would be translocated to sinks in the following proportions:-

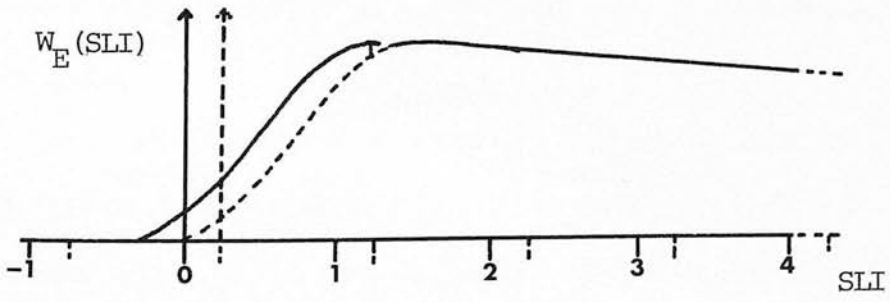
(d)



The total weight of assimilate arriving in the terminal meristem would be added to the left-hand, i.e. younger, end of W_E(SLI) to represent the expansion of new leaves. If the approximation is made that the rate of leaf extension and weight gain is linear (SILSBURY, 1970; RYLE *et al.*, 1973), then the weight increment can be distributed evenly between all expanding leaves:



The shaded area represents the total weight of assimilate translocated to the terminal meristem in an established tiller. The addition of new growth at the terminal meristem displaces older leaf material to lower leaf positions. This is simulated by moving the y-axis to the left by a distance corresponding to the time interval being used for modelling, e.g. ¼ of an SLI:



- - - - - previous distribution of W_E(SLI)

——— distribution after new weight has been added and the y-axis moved through ¼ of an SLI.

Some assimilate would be translocated to dependent daughter tillers (Fig. (d) p. 262). This weight would be added to a W_D(SLI) distribution in a similar manner to that already outlined for W_E(SLI).

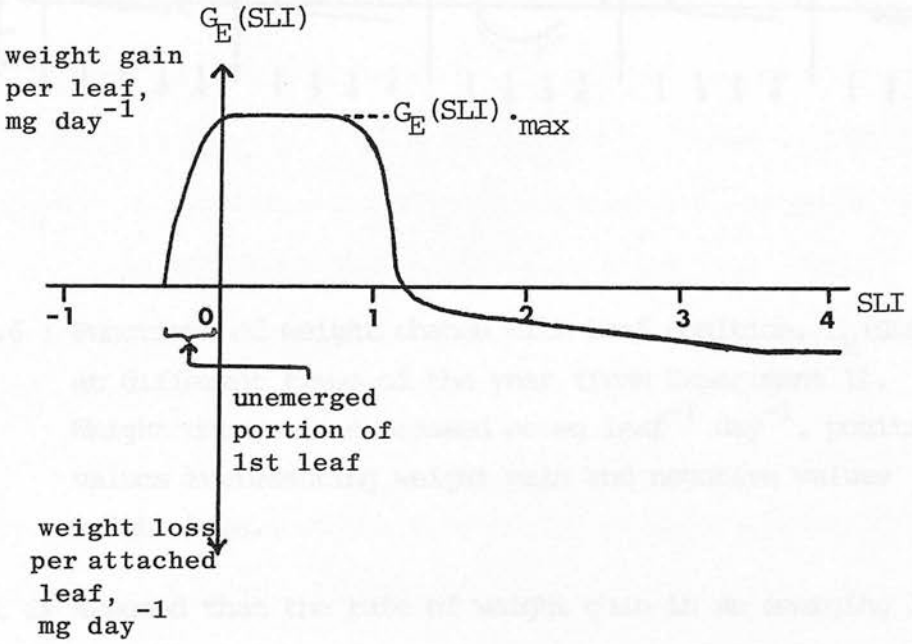
Assimilate translocated to the roots would be subtracted from the pool of current assimilate (Figs. (c) and (d), p. 262) but need not be considered further in a temperate grassland grazing model since it is not recirculated (Lit. Rev., p. 75). It is conceivable that root development might subsequently limit shoot growth, but since assimilate is partitioned to the shoot at the expense of the root in times of stress (Lit. Rev., p. 77), it seems unlikely that the root system need be taken into account.

Weight loss due to maintenance respiration can be accounted for by subtracting a constant proportion from the dry weight per SLI distribution, in the absence of more detailed evidence (RYLE *et al.*, 1973).

6.3.2 APPROACH (2) Model based on empirical weight changes

Leaf weight change on established vegetative tillers

Leaf weight change due to pasture growth and senescence will be represented by a function, $G_E(SLI)$, taking the following postulated form:



$G_E(SLI)$ is shown as increasing from 0 mg day^{-1} in very young unemerged leaves, to a constant maximum level $[G(SLI)_{max}]$ in emerging leaves. Weight gain then falls off rapidly when a new leaf emerges and the original leaf passes into the 2nd leaf position. The leaf may, as in the diagram, lose weight as it grows older.

Rates of weight gain and loss in individual leaves on vegetative tillers were calculated, in the first experiment, for different times of the year (p. 155). The relationships shown over the page for $G_E(SLI)$ were extracted from the graphs opposite p. 151:

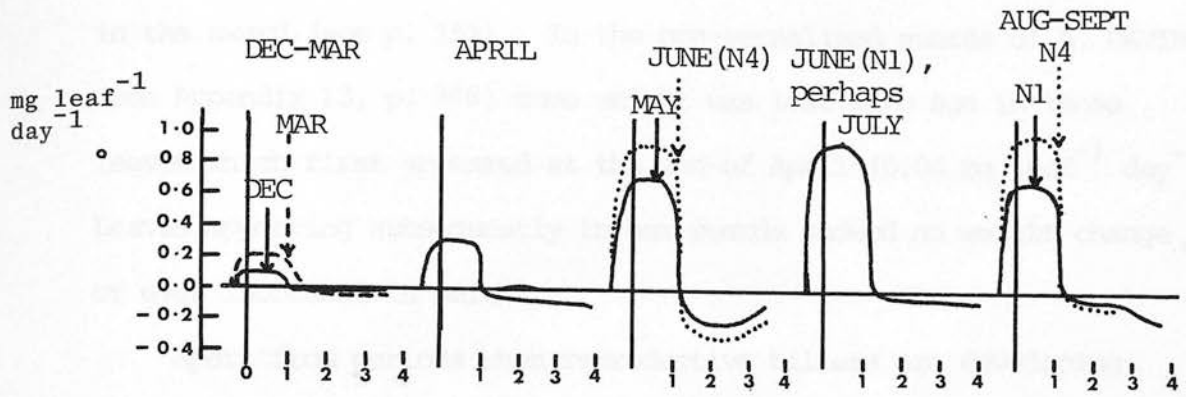


Fig. 6.6 : Functions of weight change with leaf position, $G_E(SLI)$, at different times of the year (from Experiment 1). Weight change is expressed as mg leaf^{-1} day^{-1}, positive values representing weight gain and negative values weight loss.

It is assumed that the rate of weight gain in an emerging leaf is directly related to the rate of leaf extension, and that leaves extend at a constant rate from SLI = 0 to SLI = 1 (SILSBURY, 1970; RYLE *et al.*, 1973). The evidence from Experiment 1 suggests that between February and June leaves grew faster during the later stages of their development in response to improving environmental conditions (p. 148). In the model, environmental conditions will affect the value of $G_E(SLI)_{max}$ but it is suggested that the shape of $G_E(SLI)$ between SLI = 0 and SLI = 1 will remain unaltered: it is expected that environmental factors will affect the rate of weight gain of all emerging leaves from SLI = 0 to SLI = 1 to a similar extent.

Substantial weight loss (0.06 to 0.20 mg leaf^{-1} day^{-1}), relative to the rate of weight gain, occurred in leaves of vegetative

tillers during periods when there were reproductive tillers developing in the sward (see p. 151). In the non-vernalized swards of A. DAVIES (see Appendix 13, p. 346) some weight was lost with age in those leaves which first appeared at the end of April (0.06 mg leaf^{-1} day^{-1}). Leaves appearing subsequently in her swards showed no weight change, or even increased in weight.

Apart from periods when reproductive tillers are developing, the evidence suggests, (p. 151), that in general there is little weight change in vegetative tillers once a leaf has expanded. It follows that the weight of the 1st fully expanded leaf is the parameter of prime importance in generating the function of leaf weight with leaf position (W_E(SLI)).

The weight attained by the first fully expanded leaf (2nd leaf) is influenced by seasonal factors, fertilizer application, and defoliation management.

In the field experiment, the weight of the 2nd blade was found to increase to a maximum in July and thereafter decrease to a winter minimum equal to about one-third of the July maximum. SHIM (1975) also found that the 2nd blade had its maximum weight between late June and the end of August. Maximum blade weight in July and August corresponds to ALBERDA and SIBMA's observations (1968) on leaf blade length. They found that, in a perennial ryegrass sward, blade length of successive leaves increased steadily until the end of July. In August there was a further increase in length but this was relatively small.

The results of the field experiment (Experiment 1) suggest that blade weights were little affected by the level of nitrogen fertilizer,

even when 202 Kg N ha^{-1} were applied in a single dressing. Sheaths showed a small increase in weight. However, SHIM's results (1975; Aberystwyth) indicated a substantial effect of nitrogen on fully expanded green leaf blades in June, July and August, 262 Kg N ha^{-1} leading to weight increases of between 40 and 57% under frequent (3-weekly) defoliation. There was no significant increase in blade weight in his experiment between April and May, or September to October.

One of the factors which may have influenced the results in Edinburgh was the presence of more daughter tillers in the high nitrogen swards. Inclusion of the daughter tillers in the weight samples may have hidden an effect of nitrogen on leaf weight in established tillers. It is likely that SHIM's samples tended to exclude daughter tillers since he was harvesting above a height of 4.5 cm.

Thus in the model it would appear that some allowance should be made for a positive effect of nitrogen on the weight of the second leaf in W_E(SLI), providing there is a separate compartment dealing with daughter tillers.

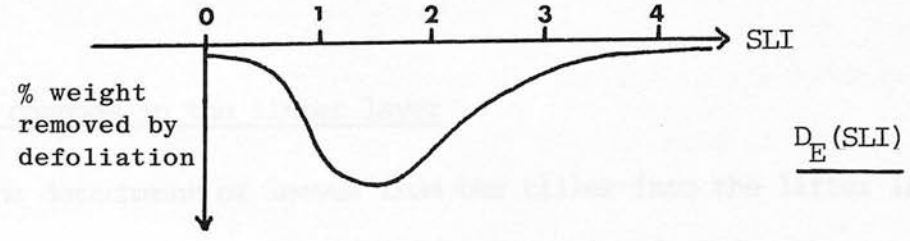
Defoliation was found to have little effect on the weight of subsequent leaves unless it included the removal of at least the 1st and 2nd blades (Experiment 2). This is in agreement with the results of DE LUCIA SILVA (1974) and A. DAVIES (1974). It has been mentioned in the Literature Review (p. 76) that the removal of the 1st and 2nd blades leads to an 83% reduction in the amount of assimilate translocated to the terminal meristem. Under moderate to severe grazing pressure, removal of both the two youngest blades is likely to occur (see p. 68) but it will be influenced by the

relative horizons occupied by leaves of different ages (see Fig. 4.3.26, p. 158). This aspect of sward structure is discussed more fully later.

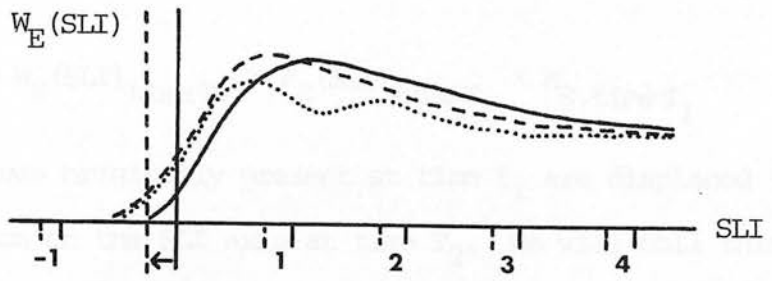
SHIM (1975) showed that the interval between severe defoliations (sward cut to 4.5 cm) had a substantial effect on weight per fully expanded green leaf blade subsequently produced. Severe defoliation every three weeks led to a 17% reduction in blade weight compared with a defoliation interval of four weeks, an aspect of pasture growth relevant to rotational grazing systems.

A pasture model should, therefore, incorporate a relationship between weight of a fully expanded green leaf and the frequency of defoliation of the individual tiller, at least in grazing systems involving high grazing pressures.

The distribution of $W_E(SLI)$ at different times of the year and under different nitrogen and defoliation regimes has been examined. The diagram on p. 265 showed how weight changes ($G_E(SLI)$) due to pasture growth and senescence, could be represented. Leaf weight losses by defoliation, $D_E(SLI)$, can be related to the distribution of $W_E(SLI)$ using the following type of function:



The two sources of leaf weight change, $G_E(SLI)$ and $D_E(SLI)$, when applied to the leaf weight distribution curve $W_E(SLI)$, will generate the new leaf weight distribution:



——— W_E(SLI) at time 1

- - - - W_E(SLI) at time 2 after leaf growth and senescence.

····· W_E(SLI) at time 2 after both leaf growth and senescence, and defoliation.

Displacement of leaves to a lower SLI position on the tiller can be simulated by shifting the y-axis to the left as shown. If the time unit being used for the model was 4 days, and the leaf appearance interval was 16 days, then the y-axis would be shifted by one-quarter of an SLI.

Weight changes in the litter layer

The detachment of leaves from the tiller into the litter layer occurs automatically in the model as a result of moving the y-axis of the leaf-weight distribution W_E(SLI) to the left at each time step, and multiplying by P_E(SLI). The weight of material passed to the litter layer at time T_2 that was present on the tiller at time T_1 is calculated as follows:

Total weight (per unit area of ground) of leaves attached to tillers at time T_1

$$= W_E(SLI)_{\text{time } T_1} \times P_E(SLI)_{\text{time } T_1} \times N_{E,\text{time } T_1} \quad (1)$$

The leaves originally present at time T_1 are displaced to an older position on the SLI axis at time T_2. We will call this displaced $W_E(SLI)$ distribution $W_E(SLI)_{\text{time } T_1.\text{displaced}}$.

Then the total weight per unit area of the original T_1 leaves that are still attached to tillers at time T_2

$$= W_E(SLI)_{\text{time } T_1.\text{displaced}} \times P_E(SLI)_{\text{time } T_2} \times N_{E,\text{time } T_1} \quad (2)$$

So total weight (per unit area) of leaf material passing into the litter layer in the period T_1 to T_2, from established vegetative tillers, equals expression (1) minus expression (2).

The weight of material added to the litter layer through the death of an established tiller would be approximately equal to $\int_{SLI=0}^{SLI_{max}} W_E(SLI)$. This is likely to give an overestimate for an individual tiller since all the leaves are dead. The death of tillers is handled by the "Tiller population changes" compartment of the model (see diagram on p. 240).

The amount of litter present on the pasture is the balance between rate of addition of new litter, and the rate of its disappearance from ground level.

In the field experiment there was an accumulation of litter (expressed as weight per tiller) in July and August 1974. Conditions at ground level were rather dry since there were moderate to severe moisture deficits in the soil itself (Fig. 4.3.3, p. 114). Litter has been observed to accumulate over the summer months in New Zealand when conditions are dry (CAMPBELL, 1964; L.A. HUNT, 1965).

The summer accumulation of litter may be further related to the reduced earthworm activity that has been observed at this time of year by J. GRANT (pers. comm.). A build-up of litter in summer has also been noted by A. DAVIES (pers. comm.).

The considerable reduction in litter per tiller in September may reflect, to some extent, the presence of a substantial number of new tillers (Table 4.3.10, p. 166) too young to have produced any litter themselves. It may also have been associated with very wet but mild weather in early September which would have favoured microbial activity. Earthworms were also much in evidence, their casts several times submerging rings on labelled tillers. WILMAN & MARES MARTINS (1977) report that approximately 59% of the senescent grass material produced from September to mid-October disappeared during the same period, whereas a smaller percentage (36%) disappeared in the August to mid-September period when the soil had been very dry.

Between January and early April the amount of litter per tiller remained fairly constant, as did tiller numbers. Leaves were dying very slowly at this time so the balance must have been maintained by an equally slow rate of litter disappearance. Litter made up 40-55% of the sward by dry weight during these months (p. 152).

Old dead leaves which are added to the litter over the winter months will be larger in size than the new leaves being slowly produced. This, together with the slow disappearance of material from the litter layer, must in part account for (1) the observed association between the percentage of "winter-burn" and the weight of herbage entering the winter, and (2) the increasing percentage of 'winter-burn' over late autumn and winter. "Percentage winter-burn"

appears to be a blanket phrase used to describe the proportion of herbage that is yellow or brown, and therefore includes both naturally senescent and frost-damaged material. Reports of the percentage of 'burnt' material in S24 ryegrass therefore range rather widely from 1% to 30% (BEDDOWS & JONES, 1958) and 43% (MILES, ap GRIFFITH & WALTERS, 1964), depending on the conditions of the observations.

In Experiment 1, temperature rose sharply towards the end of April and may indirectly have led to almost complete disappearance of the accumulated litter by early June. By June and July there was little litter present (10% of sward dry weight, Fig. 4.3.21, p. 152) even though a new leaf was appearing and an old one dying about once every 15 days. The soil was once again very dry during this period; evidence of an association between dry conditions and slow litter decay was not, therefore, supported on this occasion.

There was a consistent tendency for there to be less litter per tiller on the higher nitrogen plots although this only reached significance in early April 1975. There had been no increase in temperature at this time. Examination of litter weights in the preceeding months show that the significant difference achieved in April was a cumulative effect first started the previous autumn and perhaps gradually enhanced over the winter. In general, leaves died just as fast, sometimes faster, on the higher nitrogen plots as on the low. The different weights of litter per tiller in the high and low nitrogen treatments must therefore have been due to different rates of disappearance.

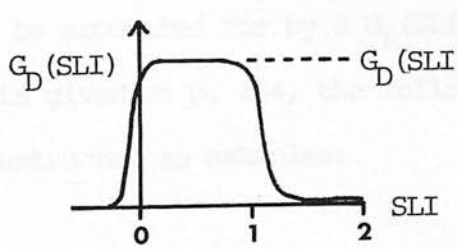
It may be that higher rates of disappearance were associated with a higher nitrogen content in dead leaves when nitrogen fertilizer is applied (WILMAN *et al.*, 1976a), promoting microbial activity and

perhaps earthworm population size. WATKIN & WHEELER (1966) found that, in the course of three years, earthworm numbers and weight increased more under a pasture fertilized with nitrochalk than in unfertilized pasture. This may have been partially related to a greater quantity of available dry matter, and partially to an increase in nitrogen content.

In the diagram outlining the model (p. 240), the litter layer has been placed in a separate compartment from the rest of the herbage. The rate at which material moves into it is determined by processes in the tiller, but the rate at which material disappears from it is independently controlled. From the preceding discussion it can be concluded that the principal factors which should regulate litter disappearance in the model will be temperature, moisture and season of the year (the latter in relation to earthworm activity). An effect of nitrogen fertilizer on litter disappearance may also be incorporated in the model.

Leaf weight change on daughter tillers: $G_D(SLI)$

Leaf weight change could be handled in the same way as on established vegetative tillers, where $G_D(SLI)_{max}$ equals the mean weight of a fully expanded leaf on class 3 daughter tillers (see p. 252), e.g.:



As with established vegetative tillers, the weight of material added to the litter layer through the death of a class 3 daughter tiller would be approximately $\int_{0}^{SLI=2} W_D(SLI)$. Weight changes associated with class 1 or 2 daughter tillers are regarded as unimportant.

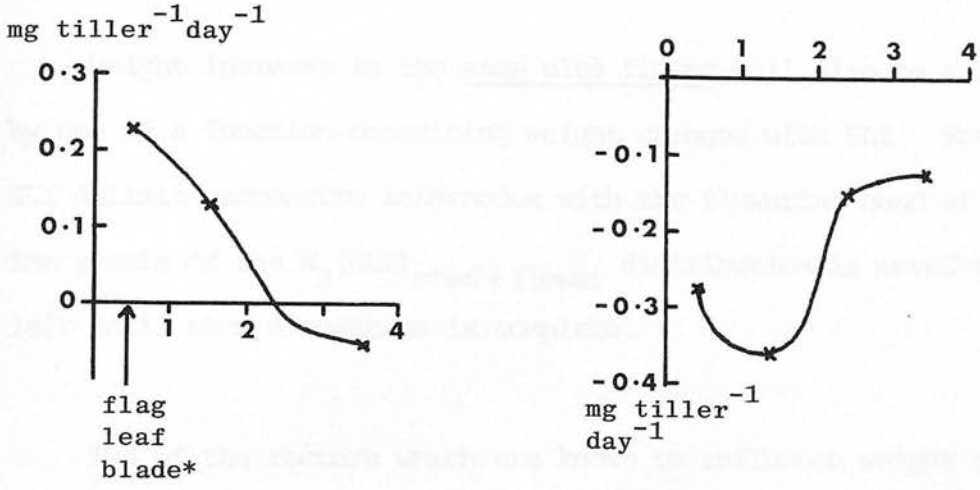
Weight change on reproductive tillers

Results from the field experiment suggest that reproductive tillers began to grow faster than vegetative tillers from the end of February onwards. The rate of weight increase must have been more than twice that on vegetative tillers because the last four culm leaves were at least twice as heavy as vegetative leaves, and they were produced in a shorter interval of time.

In the model, therefore, the initial distributions describing the weight on reproductive tillers - $W_R(SLI)_{blade}$, $W_R(SLI)_{sheath}$ and $W_R(SLI)_{stem}$ - would be developed from the vegetative weight distribution $W_E(SLI)$ as it existed in week 8.

The growth of leaf blades and weight change with age can be represented in the same way as that used for established vegetative tillers until the flag leaf has completely emerged. After the flag leaf-blade has stopped growing, the y-axis of the $W_R(SLI)_{blade}$ distribution will no longer be moved to the left to accommodate the production of new leaf material. Weight change in the blades, however, will still be accounted for by a $G_R(SLI)_{blade}$ function.

From the results given on p. 154, the following $G_R(SLI)_{blade}$ functions can be constructed as examples:



MAY 6TH TO 26TH
(blades 1 and 2
still growing)

MAY 26TH TO JUNE 3RD
(flag leaf blade fully
expanded. 50% ear
emergence on May 26th)

Fig. 6.7 : Leaf blade weight changes, $G_R(SLI)_{blade}$, on reproductive tillers (from Experiment 1, p. 154).

* - growth rate of the flag leaf blade estimated from details not presented on p. 154; the rate given is likely to be an overestimate.

The growth of sheaths and their weight changes with age can be represented in a similar manner. However, since sheath extension continues until head emergence, displacement of older sheath material to lower positions on the SLI axis of the $W(SLI)_{sheath}$ distribution will be continued until this stage is reached. Sheath extension continues after the blade has expanded, so the function $G_R(SLI)_{sheath}$ will take a rather different form:

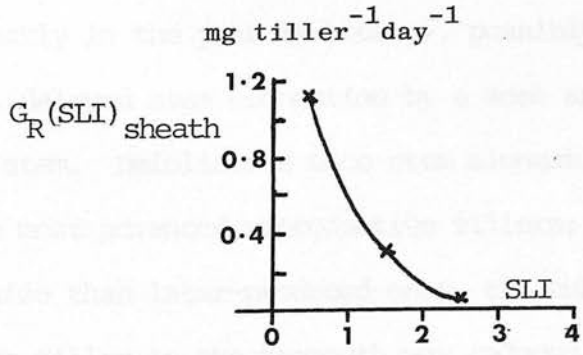


Fig. 6.8 : $G_R(SLI)_{sheath}$ calculated from Experiment 1, p. 154, May 6th - 26th.

Weight increase in the stem plus flower will also be achieved by use of a function describing weight changes with SLI. Successive SLI delimit successive internodes with the flowering head at the end. The y-axis of the $W_R(SLI)_{stem+flower}$ distribution is moved to the left until stem elongation is complete.

Two of the factors which are known to influence weight and length per reproductive tiller are nitrogen fertilizer and defoliation. The measurements of WILMAN *et al.* (1977) on stem-plus-sheaths indicate that, in primary cuts, the application of 262.5 Kg N ha^{-1} increased 'stem' weight and stem length but to an extent that depended on the time that the stem had been growing. Thus the weight difference of 38% (between 0 and 262 Kg N ha^{-1}) during the first three weeks of May, had disappeared by early June while the difference in length fell from 49% to 22%. It could be that nitrogen hastened the rate of development of the reproductive stem, as well as increased its final length.

The effect of sward cutting on reproductive stem weight at subsequent harvests is complex, depending very much on the time of the cut in relation both to the initiation of the floral apex and to the time at which the apex is raised above cutting height (I. DAVIES, 1969, pp. 24-35). DAVIES' results show that cutting the sward early in the year (February), possibly before reproductive initiation, delayed stem elongation by a week and led to greater weight per stem. Defoliation once stem elongation had started removed the most advanced reproductive tillers; since these achieve a greater size than later-produced ones, the subsequent weight per reproductive tiller in the regrowth was reduced.

In the field experiment, reproductive tillers showed a very great net increase in weight per day during the period May 6th to May 26th (50% ear emergence) (p. 154 : 4.6 to 5.8 mg tiller^{-1} day^{-1}). About one-third of the gross increase in weight during this period was due to increase in the weight of leaf, half of this being blade and half sheath (Fig. 4.3.22b, p. 153). Greatest weight gain was, of course, due to development of the stem and inflorescence.

The importance of quantifying reproductive tiller growth in the pasture model is indicated by the relative gross crop growth rates of vegetative and reproductive tillers. Gross crop growth rate was calculated as the rate of production of new material per tiller (see Table 4.3.8, p. 151), multiplied by the number of tillers per metre^2. On May 5th 1975, in the lowest nitrogen treatment, vegetative tillers were contributing 22 Kg ha^{-1} day^{-1} to the sward while reproductive tillers (43% of the tiller population) were producing 106 Kg ha^{-1} day^{-1}.

Gross crop growth rates for the lowest nitrogen treatment at other times of the year were also calculated where some estimate could be made of tiller numbers:-

14. 8.74	47	Kg	ha^{-1}	day^{-1}
17. 1.75	7	"	"	"
4. 3.75	8 to 10	"	"	"
7. 4.75	9 to 13	"	"	"
5. 5.75	128	"	"	"
7. 6.75	69	"	"	"

Gross crop growth rates thus appear to be greatly influenced by the presence of reproductive tillers in the sward and their stage of growth. I.DAVIES (1969, p. 30) pointed out the major contribution that reproductive tillers made to yield differences between alternative

cutting treatments. The stage of growth of reproductive tillers also has a profound effect on their digestibility (see p. 143 and Lit. Rev., p. 62) which begins to decline before reproductive tillers have ceased their rapid phase of growth. Clearly a grazing model should be amenable to investigation of the factors involved in management decisions made at such critical periods.

The limited information obtained in Experiment 1 on reproductive tillers highlights their very great importance even in swards which are managed for grazing. There appears to be relatively little information available in the literature on specifically reproductive tillers in perennial ryegrass that could be used for modelling reproductive growth at the structural level required for grazing studies. Further investigations are necessary, though a major difficulty in following early reproductive growth is that of knowing in advance which tillers are reproductive without first pulling them up and disecting them.

5.3.3 Rate of Leaf Appearance

In the empirical model of weight change (as opposed to the carbon metabolism model of RYLE *et al.*) the weight of material added per day to the younger end of the W(SLI) distribution is derived from the weight of a fully-emerged leaf divided by the length of the leaf appearance interval. The addition of new material to the younger end of the W(SLI) distribution simultaneously moves older material to lower leaf positions (p. 270). The rate of leaf appearance (reciprocal of the length of the leaf appearance interval) must therefore be predicted in the empirical weight changes compartment of the model (Compartment K_2, Fig. 6.1, p. 240).

Leaf appearance on established vegetative tillers

Seasonal changes in leaf appearance

Leaf appearance interval in the field experiment changed with day-length. There was no consistent relationship with temperature or sunshine hours.

A strong correlation between day-length and rate of leaf appearance has already been noted by PATEL & COOPER (1964) working with seedlings grown in a greenhouse at different times of the year. To some unknown extent, the correlation may have been associated with the corresponding changes in total light energy, but the evidence suggests that photoperiod itself was an important regulating factor. There was no relationship with temperature over the course of the year.

Outdoors, ROBSON (1967) working with *Festuca arundinacea* has found that leaf appearance was at its slowest in December even though weather conditions were poorest in January and February. A. DAVIES (1977) has drawn together results from numerous experiments done in different years; she found that the slowest rate of leaf appearance of S23 and S24 ryegrass occurred a little later, in January. I. DAVIES (1969) also found the slowest rate of leaf production in S24 was in December or January. The association observed in the field between leaf appearance rate and day-length does not generally occur in indoor comparisons between different fixed photoperiods (e.g. PATEL & COOPER, 1961; RYLE, 1966; ANSLOW, 1966).

The rate of change in day-length therefore appears to be implicated in the control of leaf appearance rate. Endogenous physiological cycles approximately 24 hours in length are of

common occurrence in plants and animals (BÜNNING, 1967). The phases of the endogenous rhythms are 'entrained' to specific lengths by external diurnal cycles, particularly the day-night cycle. BÜNNING suggests mechanisms by which plants and animals can respond to a change in day-length, and can distinguish between increasing and decreasing day-length.

The slowest rate of leaf appearance in Edinburgh was 1 leaf every 50 to 55 days from November to mid-February. This rate is similar to that measured by I. DAVIES (1969, Aberystwyth) but much slower than that of A. DAVIES (1977 : 35 days, Aberystwyth). I. DAVIES' figures are taken from one year's observations (1963-64), whereas those of A. DAVIES are from several years. It may be that in general the milder climate on the west coast leads to faster rates of leaf appearance than in south-east Scotland. It has been found that there is a close regression of leaf appearance rate on temperature at ground level out-of-doors between May and October (THOMAS, 1975). It was not possible to ascribe this solely to temperature since light intensity and duration were also varying in a seasonal manner. Growth room experiments have also indicated a strong influence of temperature on leaf appearance rate (ANSLOW, 1966).

Between February and April leaf appearance increases rapidly until it reaches a rate of about 1 leaf every 15 days on vegetative tillers (I. DAVIES, 1969; A. DAVIES, 1977; Experiment 1, p. 120).

During the summer months in the field experiment (weeks 17 to 34), the rate of leaf appearance on vegetative tillers varied

between 1 leaf every 10 to 1 leaf every 20 days. It was fastest in April - May and in late August. The slowest rate, of 1 leaf every 18 to 20 days, occurred during the July 'trough' of pasture growth (see p. 30).

Effect of reproductive tillers on leaf appearance in vegetative tillers

After flag leaf emergence, leaf appearance on vegetative tillers was slower in a sward containing reproductive tillers than in one in which reproductive apices had been removed by cutting (see p. 120). Tiller bud development is also suppressed during stem elongation (LANGER, 1974). LANGER suggests, on the basis of his and other experiments, that hormones cause assimilate to be transported to the stem at the expense of tiller buds and axillary tillers. The observations just mentioned from Experiment 1 suggest that the demand for assimilate by the reproductive stem may inhibit growth of adjacent vegetative tillers, and slow down the rate at which new leaves are produced.

Effect of nitrogen fertilizer on leaf appearance

Nitrogen fertilizer increased the rate of leaf appearance for six to eight weeks following its application (Experiment 1, p. 121). This effect has also been reported by MORRIS (1967) and I. DAVIES (1969).

Effect of defoliation on leaf appearance

Defoliation may increase or decrease the rate of leaf appearance through its effect on a number of factors, e.g. assimilate supply, temperature at the apex, and sheath tube length (Lit. Rev., p. 80). There was little effect of defoliation in the field experiment. After the sward was cut, the rate of leaf appearance followed the

same course of change as was apparent before the cut (see Fig. 4.3.4, p. 120), except on the occasion which has already been described when many reproductive tillers were removed.

In the second experiment, even the removal of all the leaf blades had no effect on rate of leaf appearance. It had been expected that defoliation would limit assimilate supply and therefore reduce the rate of leaf appearance, but this expectation was not fulfilled; only the weight of the leaves was reduced and this effect was substantial.

These results differ from those of A. DAVIES (1974) who found that removal of both the two youngest leaves led to a 28% reduction in rate of leaf appearance from 1 leaf every 5.6 days to 1 leaf every 7.7 days. DE LUCIA SILVA (1974) measured a reduction in leaf appearance when the 2nd and 3rd leaves were removed, but not the 1st and 2nd. Both these authors were working with spaced plants grown in nutrient solution (DAVIES) or soil (DE LUCIA SILVA). The differential defoliation experiment reported here was, on the other hand, carried out on dense seedling swards under low light intensities and cold night temperatures, and it may be that the rate of leaf appearance was limited for other reasons.

Leaf appearance on daughter tillers

It is not known whether leaf appearance takes place at the same rate on daughter tillers as on established vegetative tillers.

Leaf appearance on reproductive tillers

Leaf appearance on reproductive tillers (I. DAVIES, 1969) and in vernalised swards (A. DAVIES, 1971b) is faster than in purely vegetative material in April and May respectively. In Experiment 1 this difference was found to be confined to the last three culm leaves only.

Summary

For the purpose of predicting leaf appearance rate in the model, therefore, it appears that the most important variable involved may be day-length. The influences of temperature and nitrogen must also be taken into account but their effects are regarded as modifications of a basic rate of leaf appearance possibly governed by day-length.

6.4. DIGESTIBILITY OF SWARD COMPONENTS AND OF THE SWARD

6.4.1 Digestibility of sward components

In the Literature Review, the differences in cell structure and content between blades, sheaths and stem were discussed in terms of the consequences they might have for the digestibility of these organs. Changes in cell composition that take place with age were also examined. The digestibilities measured in Experiments 1 and 2 will be discussed here in relation to the literature review before going on to consider the representation of digestibility in the pasture model.

Leaf blades

Experiment 1 showed that leaf blades did not change much in digestibility whilst they were completely green. The 1st leaf was always a little (1 - 4 units) more digestible than the 2nd blade, except at the end of June in each year. The slightly higher digestibility of the 1st leaf compared with the 2nd blade may be associated with the enclosed portion of the leaf. This portion is unlikely to have developed a cuticle (WILSON, 1976b) and may undergo some lignification and slight increase in percentage cell wall content (HARTLEY, 1972) as it expands, emerges and matures.

The low digestibilities of the 1st and 2nd leaves in late June of each year, and of the 3rd leaf in 1975, might possibly have been associated with the high temperatures recorded at a depth of 5 cm into the soil (and therefore probably even higher temperatures at the level of the stem apex). Thus DEINUM & DIRVEN (1971) found that a rise in temperature from $15^{o}/10^{o}C$ to $20^{o}/15^{o}C$ resulted in a higher cell wall content, including more lignin, and a 5 unit digestibility fall. In the second experiment reported here, the

very low digestibilities of the young leaves in the 20°C room (1st leaf = 73% IVOMD) may also have been related, to some extent, to the high daytime temperature. However, in the field, 1st and 2nd leaf digestibilities increased in August although high temperatures (and also severe soil moisture deficits) persisted.

High digestibilities of the 1st (emerged portion) and 2nd leaf blades have been measured by I. DAVIES (1969) in early October (83.5 and 79% IVDMD respectively). These values are similar to those measured in Experiment 1 (87% IVOMD for emerged + unemerged portions of the 1st leaf, 84% for the 2nd blade) at the same time of year. There are no other reports in the literature on digestibilities of leaves at different positions with which to compare the measurements made in the field experiment.

The 1st to 3rd leaves were still very highly digestible in early November. This may account for the very high digestibilities of monthly regrowths cut in November, cut to a height which may have excluded the rapidly declining digestibilities of the 4th leaf and litter layer (MINSON *et al.*, 1960; DENT & ALDRICH, 1968). The very slight but persistently lower digestibilities of 1st and 2nd leaves from December to March (Experiment 1) may have been related to the low light intensities at this time of the year.

In general leaf blade digestibility began to fall markedly once the leaf started to lose colour. The fall corresponds to the changes in leaf structure and content that have been noted in the literature as occurring at this time, *viz* collapse of thin-walled tissues (Lit. Rev., p. 57, JOHNSTON & WAITE, 1965) and the (presumably) associated rise in cell wall content (p. 58; HARTLEY, 1972). The nutritive value of the leaves changes in other ways as

well at this time, notably in their crude protein content (pp.37-38, 57), and in their mobilisable mineral and nitrogen contents (p. 41).

Once leaves had turned brown or 'dead', their digestibility still continued to fall to a considerable extent. In the 5°C and 10°C growth rooms, leaves attained their minimum digestibility of about 26% by 3 to 3½ leaf appearance intervals after they had turned completely brown. The lowest digestibility recorded in the field, for the litter layer, was about 32%.

Leaf sheaths

Second and 3rd sheaths were always 2 - 9 units higher in digestibility than their corresponding blades on vegetative tillers, apart from the 3rd leaf in March 1975. The higher digestibilities of the 2nd and 3rd sheaths compared to their blades may be related to the accumulation of fructosan (EAGLES, 1967a) and to the delay in cuticle development until the tissue surface becomes exposed to the atmosphere (WILSON, 1976b). The 4th sheath was found to be similar in digestibility to the 4th blade on the only occasion (June 1975) that the parts were analysed separately.

The digestibility of the 3rd sheath fell steadily and substantially over the winter. This was presumably related to the earlier onset of leaf colour change. However, while 3rd blade digestibility reached a minimum (70%) in December, the sheath reached its minimum (70%) later, in early March (see p. 138). The difference between blade and sheath might be explained if sheaths died (lost their green colour) some time later than blades. The time lapse between December 17th and March 3rd corresponds to about one-and-a-half leaf appearance intervals. However, the date on which a leaf sheath lost its green colour was not recorded in this experiment.

According to SOPER & MITCHELL's anatomical measurements (1956-7) on young vegetative ryegrass tillers, one would expect sheath digestibility to decline sooner and further than in the blade (Lit. Rev., p. 60). Neither of these suppositions was upheld in vegetative tillers from the field experiment. The case was different in reproductive tillers (p. 143). Sheaths fell very quickly in digestibility while both they, and the stem, were elongating. This agrees with JOHNSTON & WAITE's observations. (Lit. Ref., p. 62).

Stem

Prior to head emergence in the field experiment, stem digestibility fell by 14 units from 89.5% to 75% IVOMD when 10% of the heads had emerged (0.91 IVOMD units day^{-1}). This drop may have been brought about partly by the deposition of lignin which JOHNSTON & WAITE (1965) measured chemically as forming apparently 5% of the dry weight by the onset of head emergence, although their staining and histological examination failed to show its presence. Since JOHNSTON & WAITE also measured a large increase in fructosan content (100% digestible) during this period, it would appear that substantial structural changes must have taken place in the cell walls by the onset of head emergence in order to account for the large fall in digestibility.

From head emergence onwards, the analyses carried out on stem show digestibility changes similar to those reported and explained by JOHNSTON & WAITE (1965). The digestibility of the stem at head emergence (75% IVOMD) was similar to that measured by JOHNSTON & WAITE (76 - 78%) and it remained steady, as did theirs, for about 10 days whilst the rest of the heads were emerging. This maintenance of a high level of digestibility (which occurred in the rest of the

tiller as well) over a 10 day period from the first signs of head emergence is important. It both gives a farmer an easily identifiable indication of the onset of this period, and some flexibility in deciding on which day to cut for conservation during the ensuing 10 days.

It is apparent from the literature reported on p. 60 that the successive internodes and head differ from one another both in digestibility and rate of change in digestibility. This suggests that their digestibilities should be described individually for the purposes of a grazing model.

Litter

Digestibility of the litter layer is determined partly by the digestibility and type of material moving in to it, and partly by the lapse of time before the material disappears. The litter was always at least 20 units lower in digestibility than the 4th leaf (Fig. 4.3.14, p. 137), even when 4th leaves were completely brown. Mean digestibility of the litter layer ranged widely from around 55% IVOMD in June to 32% in early March. Some of the litter in March was likely to have been four or more months old: the substantial accumulation of litter by January was not reduced again until May even though the rate of addition of new litter was very slow (see p. 272).

In contrast, in June and July material passed in and out of the litter layer before there had been sufficient time for it to be decomposed to the fibrous skeleton, presumably because it had been dragged down into the soil by earthworms.

Effect of nitrogen on digestibility

Nitrogen fertilizer was found to reduce the digestibility of the 1st and 2nd leaves by 2 - 4 units in the first few weeks following its application. The inverse relationship between the inorganic nitrogen and water-soluble carbohydrate content of plant tissues (Lit. Rev., p. 36) suggests the possibility that the digestibility difference between young leaves of low and high nitrogen treatments might be due to a decrease in water-soluble carbohydrate content. A reduction in the water-soluble carbohydrate content of emerging, but not older, leaves following nitrogen fertilizer application was found by I. DAVIES (1969).

Nitrogen reduced the lifespan of leaves appearing just before, or up to 4 weeks after, the time of its application. This effect has also been reported by MORRIS (1967) and I. DAVIES (1969). Thus, following the August application of nitrogen fertilizer, leaves in the high-N (N4) plots lost their green colour some 2 to 3 weeks sooner than leaves on low-N (N1) plots from late October until mid-March, resulting in a difference in the number of live leaves per tiller on N1 and N4 plots (Fig. 4.3.7, p. 126). The earlier colour change in leaves on high-N plots relative to low-N plots did not, however, show up as a difference in average digestibility of the 3rd blade.

In Experiment 1 it was noted that there was a greater proportion of reproductive tillers in the regrowth of a sward to which higher levels of nitrogen fertilizer had been applied (p. 164). The rapidly decreasing digestibility of reproductive material following head emergence could therefore lead to lower sward digestibilities under high N and infrequent defoliation, as WILMAN *et al.* (1976b) have

found. The effect of nitrogen on the relative proportions of stem and leaf is taken into account by the pasture growth section of the model.

Effect of defoliation on digestibility

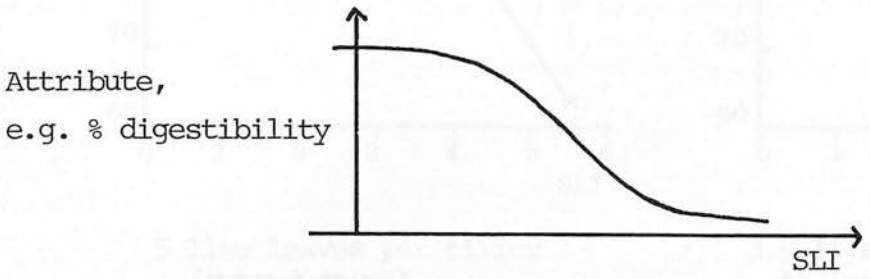
Defoliation of increasing severity in the 2nd experiment had no effect on the digestibility of leaf blades already present or produced after defoliation. In the field the patterns of change in digestibility of tiller parts bore no relation to the 4 cm sward cuts. It is therefore unnecessary to include defoliation as a factor influencing tissue digestibility in the pasture model.

6.4.2. Representation of digestibility in the pasture model

From the preceding examination of digestibility differences it is concluded that a distinction should be made in the model between leaf blades, sheaths and stem; between sheaths on vegetative and on reproductive tillers, and between leaves at different positions on the tiller. The differences in *in vitro* digestibility between these various categories are sufficiently large to affect animal intake and therefore suggest that the use of separate digestibility distributions for blades, sheaths and stem would be advisable. Differences in rate of passage due to cell wall structural differences modify the *in vivo* digestibilities of these plant parts and the amount ingested.

In the first part of Chapter 6 a framework has been developed that will pass material through a pasture from its appearance as new tissue to its disappearance from the sward. This same framework can be used to describe properties of the sward components other than their weights.

Any attribute that varies with leaf position, such as digestibility, can be described by the following type of function:



The litter layer is assigned its own mean value of the attribute.

Empirical relationship between digestibility and leaf position

Both Experiments 1 and 2 show that the digestibility of emerging leaves is very high, and that the digestibility of successively older leaf blades appears to be associated with the leaf position at which they lose their green colouration. The association was found in both vegetative and reproductive tillers. Thus from the field experiment we can draw four generalised digestibility distributions with leaf position: (see over page)

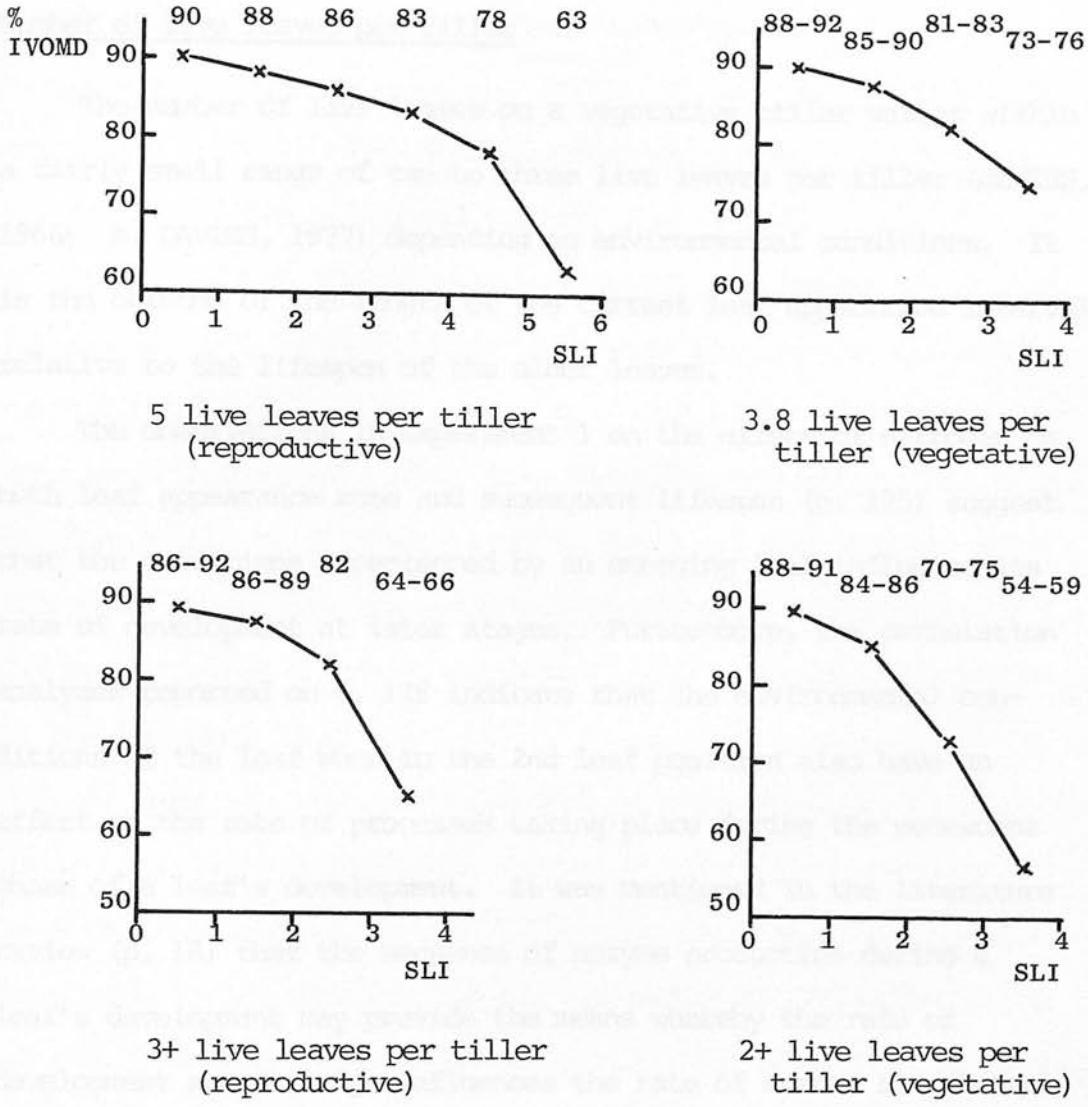


Fig. 6.9 : Digestibility of leaf blades. Field experiment, lowest nitrogen treatment (N1).

The association between leaf colour and digestibility was also found in Experiment 2. At both $5^{o}/3^{o}C$ and $10^{o}/4^{o}C$ there were 2+ live leaves per tiller. The digestibility pattern was similar to that in the 2+ distribution shown above except that the values were generally 3 to 5 units lower (1L = 86 - 87%, 2B = 80 - 82%, 3B = 68 - 72%, 4L = 44 - 49%). In order to decide which digestibility distribution to use on a particular occasion in the model, it is therefore necessary to know the number of live leaves per tiller.

Number of live leaves per tiller

The number of live leaves on a vegetative tiller varies within a fairly small range of two to three live leaves per tiller (JEWISS, 1966; A. DAVIES, 1977) depending on environmental conditions. It is the outcome of the length of the current leaf appearance interval relative to the lifespan of the older leaves.

The observations in Experiment 1 on the effect of nitrogen on both leaf appearance rate and subsequent lifespan (p. 125) suggest that the conditions experienced by an emerging leaf influence its rate of development at later stages. Furthermore, the correlation analyses reported on p. 128 indicate that the environmental conditions of the leaf when in the 2nd leaf position also have an effect on the rate of processes taking place during the senescent phase of a leaf's development. It was mentioned in the literature review (p. 16) that the sequence of enzyme production during a leaf's development may provide the means whereby the rate of development at one stage influences the rate of events at a later stage.

In the field experiment it was frequently observed that the appearance of one leaf occurred within two days of the complete death of the oldest leaf. In view of the constancy of the number of live leaves over several weeks at certain times of the year (Fig. 4.3.7, p. 126; A. DAVIES, 1977), it is logical to expect this association. The close concurrence of the two events suggests the possibility of a tight hormonal link between processes in different parts of the tiller.

It appears, then, that the narrow range in live leaf number per tiller, and the characteristic values associated with a species,

could be due to a relationship between leaf appearance rate and subsequent lifespan (see also I. DAVIES, 1962). The relationship must alter with the time of year, since the number of live leaves per tiller follows a seasonal pattern (Fig. 4.3.7, p. 126; A. DAVIES, 1977). Generally the number of live leaves per tiller appears to be relatively little influenced by nitrogen application or defoliation (I. DAVIES, 1969; A. DAVIES, 1977). In winter in Experiment 1 there were fewer live leaves per tiller on the high nitrogen plots (p. 127) as a result of reduced leaf lifespan of the older leaves, but the difference involved (2.4 compared with 2.7 on the lowest N plots) was not reflected by a lower digestibility in the senescent (3rd) blade.

In order to establish the number of live leaves on a particular occasion in the grazing model, therefore, it is suggested that a two-dimensional array describing the numbers in each month of the year would be adequate for the purpose required. Given the number of live leaves per tiller, the appropriate digestibility distributions for the blade and the sheath would then be selected. A vector would also be used to show the number of live leaves on reproductive tillers. The time scale used on this vector, however, would not be directly related to the time of the year but rather to the number of days before or after heading since the number of live leaves per tiller is closely related to this (Fig. 4.3.12, p. 134; I. DAVIES, 1969).

The values for the number of live leaves per tiller under the conditions of Experiment 1 are shown in Fig. 4.3.7 for vegetative tillers and Fig. 4.3.12 for reproductive tillers.

The representation of stem and reproductive sheath digestibility in the model requires a more complex approach since digestibility alters at a different rate in upper and lower internodes (Lit. Rev., p. 60). The simplest approach would be to have a separate function for each internode, each sheath, and the head itself. The function would describe the change in digestibility of that part with age, or in relation to the number of days before or after head emergence.

The following diagrams have been drawn from results of I. DAVIES (1969) (internodes of S48 Timothy) and Experiment 1 (sheaths and inflorescence of S24 ryegrass):

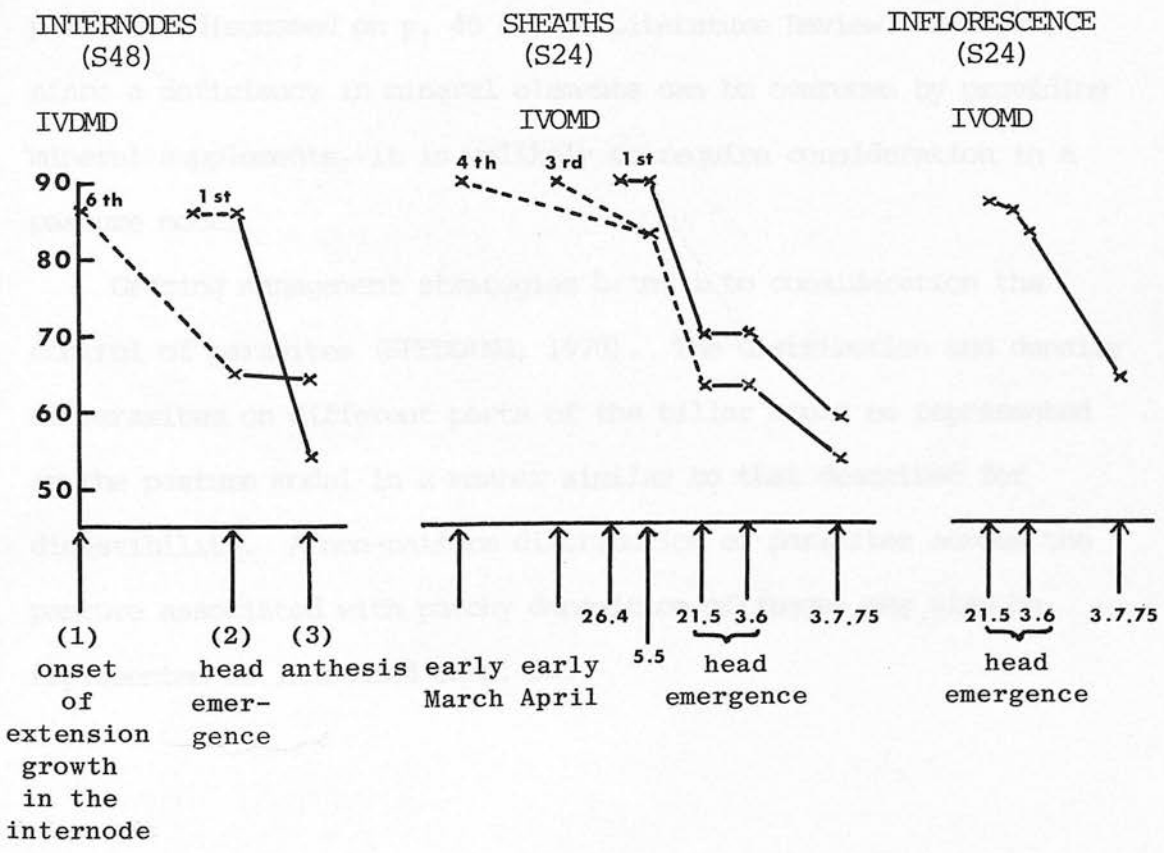


Fig. 6.10 : Digestibility changes in parts of the reproductive tiller. Dotted lines lead from assumed values, full lines from measured values. The lines show the course of digestibility change in the 6th (oldest) and 1st (uppermost) internodes of S48 Timothy; the 4th (older), 3rd and 1st (uppermost) sheaths of S24 ryegrass; and the inflorescence of S24 ryegrass.

6.4.3 Representation of other parameters of nutritional or clinical importance

The distributions of crude protein or mineral content between different parts of the plant may also be accommodated in a pasture model when examining systems where they are likely to be limiting. In temperate grazing systems there is unlikely to be a shortfall in crude protein unless the sward is allowed to develop beyond the head emergence stage in reproductive tillers. The crude protein content of sheaths and stem of reproductive tillers falls below animal requirements before (stem) or shortly after (sheaths) head emergence in S24 ryegrass (JOHNSTON & WAITE, 1965).

The distribution of minerals between different parts of the plant was discussed on p. 40 of the Literature Review. However, since a deficiency in mineral elements can be overcome by providing mineral supplements, it is unlikely to require consideration in a pasture model.

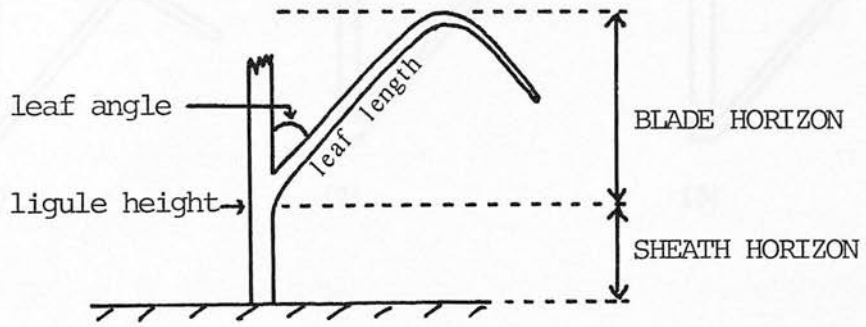
Grazing management strategies bring into consideration the control of parasites (SPEDDING, 1970). The distribution and density of parasites on different parts of the tiller could be represented in the pasture model in a manner similar to that described for digestibility. A non-uniform distribution of parasites across the pasture associated with patchy deposition of faeces may also be represented as indicated on p. 305.

6.5 SPATIAL ARRANGEMENT OF SWARD COMPONENTS

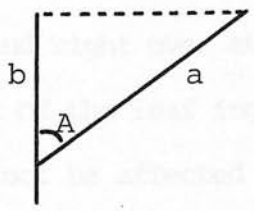
The vertical distribution of material in the sward was described in the field experiment in terms of the upper and lower boundaries of the horizon occupied by each part of the plant (section 4.3.3.4, p.155). The distribution varied enormously with season, nitrogen fertilizer application and leaf position. The following discussion examines the parameters that may be used to model the spatial arrangement of the sward components, bearing in mind that the representation must be very susceptible to environment and management.

The parameters determining spatial distribution

The horizon occupied by a leaf is determined by leaf length, leaf angle, whether or not the blade bends over, and insertion (ligule) height:



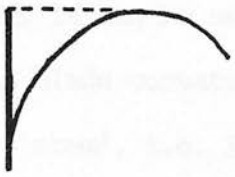
If the blade does not bend over, then weight per unit height is a linear function of weight per unit length:



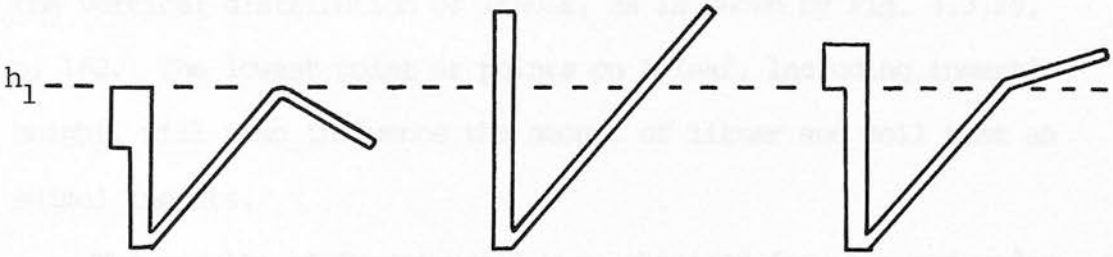
A = leaf angle to the vertical
a = weight per unit length
b = weight per unit height

then $b = a \cos A$

If the leaf does bend over, then weight per unit height would be derived from projecting a curvilinear function on to the vertical axis:



In the following illustrations, the curvilinear leaf is approximated by two straight lines and compared with the same leaf when the bend is ignored. For illustration, the leaf blade is taken to bend two-thirds of the way along its length.



(1) (2) (3)

If an animal grazed to a depth shown by h_1, then in practice it would not ingest any of the leaf shown (1). If, in the model, the bend was ignored, then the animal would ingest one-third of the weight of this blade (2). If the blade only curved but did not bend right over at height h_1, then in this particular case the amount of the leaf ingested by an animal grazing to height h_1 would not be affected (3).

The consequences of ignoring leaf curvature would be to distort the relative horizons of leaves with differing digestibilities.

This would have a significant effect on the model's estimate of the digestibility of the animal's intake, and therefore on its weight of herbage intake.

From the diagram on p. 298 it can be seen that the fixed point in an equation describing leaf blade curvature is the height of insertion of the blade on the 'stem', i.e. ligule height. The height of insertion of the blade may affect its accessibility to the grazing animal, particularly cows which cannot graze as close to ground level as sheep. The height of insertion will have little effect on the relative horizons occupied by leaves from different leaf-positions on vegetative tillers. In reproductive material, however, sheath length is a very important parameter in describing the vertical distribution of leaves, as is shown by Fig. 4.3.29, p. 162. The lowest point or points on a leaf, including insertion height, will also influence the amount of litter and soil that an animal ingests.

The results of Experiment 1 were obtained from a sward under a lax cutting regime, but will be used here to illustrate the factors involved in the approach suggested for representing sward structure. The spatial distribution of dry matter in the sward requires further examination in a grazing context.

Leaf curvature

There is no data available on leaf curvature, a parameter which will vary with tensile strength, leaf weight, treading and windspeed. In the higher nitrogen treatments of Experiment 1 it was observed that the leaves were longer and softer and tended to fall over, while those in the lowest nitrogen treatment were shorter, stiffer and more erect.

Leaf insertion height

The height of leaf blade insertion in the field experiment showed little change with season (p. 156) under a low (N1) nitrogen treatment. It increased 2½ to 3 times in seven weeks following the highest application of nitrogen, an observation supported by I. DAVIES (1969). Sheath height (leaf insertion height) is also affected by defoliation height and frequency (I. DAVIES, 1969; A. DAVIES, 1977).

Leaf length and leaf weight

The uppermost boundary of a leaf's horizon changed a great deal with season, nitrogen fertilizer application, and leaf position. Much of this variation is accounted for in the model by the component dealing with leaf weight, since leaf length is correlated with leaf weight (BAKER & JUNG, 1968; DE LUCIA SILVA, 1974). Any variation that is not accounted for will be related to changes in weight per unit length, and leaf angle.

Weight per unit length

The relationship between weight per unit height and weight per unit length was demonstrated on p. 298. It has just been explained that weight per unit height can be represented by the more basic parameters of leaf weight and weight per unit length.

Weight per unit length changes with leaf position. Young blades (1st and 2nd) were found to have a 25% greater weight per unit length than older leaves (DE LUCIA SILVA, 1974, S24 ryegrass). A similar loss in weight per unit length was measured in the 2nd experiment as leaves aged from the 2nd to 3rd leaf position in the $5^{o}/3^{o}C$ and $10^{o}/4^{o}C$ environments.

Some estimate of the effect of season can be made from the 1st experiment as follows: the height of the 1st leaf (emerged +

unemerged portions) would have been approximately equal to its length, since it did not bend over much. Division of 1st leaf height by 1st leaf weight suggests that weight per unit length of a half-emerged leaf in winter was about three-quarters of that in midsummer. THOMAS (1975) measured weight per unit length of fully emerged leaves in simulated swards transferred outdoors in successive batches. He found that weight per unit length tended to decrease with a rise in temperature and increase with radiation, with the result that there was no consistent seasonal pattern. The range during the months of May to October was substantial, from 67 to 95 mg m^{-1}. A similar trend with temperature was observed in the growth room experiment, although weights per unit length were lower in absolute value (40 to 60 mg m^{-1}).

Nitrogen fertilizer appears, in Experiment 1, to have had a very large effect on weight per unit length of both blade and sheath since it had a large effect on weight per unit height (Fig. 4.3.27, p. 159). Leaf heights were increased very much more than leaf weights by the nitrogen treatments. About seven weeks after the May application, weight per unit height of the younger leaves on the high (N4) nitrogen plots was about half that on the low (N1) plots. These results contrast strongly with those of WILMAN *et al.* (1977) whose results indicate that nitrogen led to a decrease in weight per unit leaf width but not per unit leaf length.

Leaf angle

Few measurements have been made of leaf angle at different times of the year outdoors (A. DAVIES, 1977; a review). In Experiment 1, leaf angle of the first fully emerged leaf appears to have been about 60^{o} to the vertical in winter and more acute in summer (p. 161).

The angle does not seem to have increased in winter at lower positions on the tiller, but in early summer a combination of leaf angle and leaf bend led to older leaves occupying a lower stratum in the sward. In late summer, older leaves once again appear to have been more erect.

In May to June and August to September, mean leaf angle was recorded as about 25° to the vertical by A. DAVIES (1971a), individual angles varying from 16 to 59°. Following a sward cut, most leaves were held at a small angle to the vertical but during later stages of regrowth a wide range of angles was present.

Summary

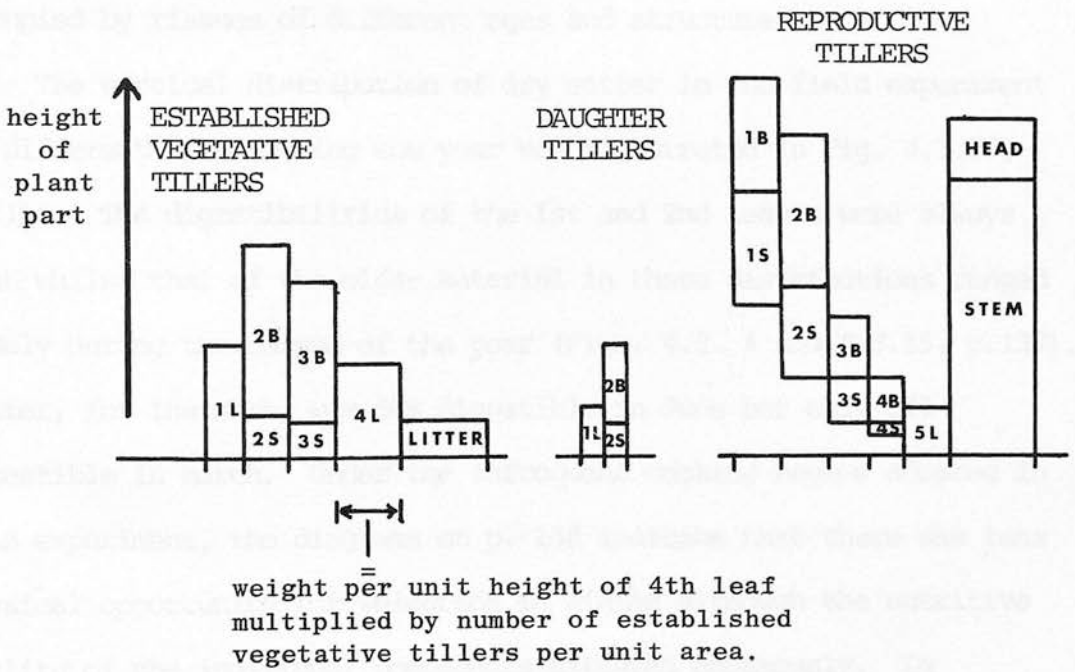
In the model, the vertical distribution of the parts of the plant will be derived from (1) their length (weight divided by weight per unit length) and (2) - in the case of leaf blades - an equation relating the horizon occupied by a leaf to its length, its angle of curvature, and its insertion height on the tiller. The small amount of information available on leaf angle, and the absence of any on leaf curvature, may prove a serious drawback.

6.6. GRAZING FROM THE PASTURE MODEL

The pasture growth section of the model generates new leaf weight and passes this weight through leaf appearance interval classes and the litter layer until it disappears from the sward.

The pasture structure section of the model describes attributes of this weight - its nutritive value and its vertical distribution in the sward.

Prior to grazing the pasture, the structure of the sward is first 'summarised' in the form used earlier in Fig. 4.3.26, p. 158, i.e.



The diagram shows the distribution of dry matter in the sward, in terms of height and weight per unit height of each part of the tiller.

The animal is then made to remove weight from this summarised pasture structure in one of a number of ways:

(1) by active selection for particular parts of the plant and for particular tillers (i.e. daughter, established vegetative, or reproductive);

(2) by passive selection, i.e. grazing the sward in layers;

(3) by grazing in patches;

(4) by some combination of (1), (2) and (3).

Animals tend to graze the sward in progressive layers from the top down, and may actively select within and between layers (section 3.3). The quality of the herbage that the animal removes will therefore be strongly influenced by the relative depths of the sward occupied by tissues of different ages and structure.

The vertical distribution of dry matter in the field experiment at different times during the year was illustrated in Fig. 4.3.26, p. 158. The digestibilities of the 1st and 2nd leaves were always high whilst that of the older material in these distributions ranged widely during the course of the year (Figs. 4.3.14 and 4.3.15, p.137). Litter, for instance, was 56% digestible in June but only 32% digestible in March. Under the infrequent cutting regime adopted in this experiment, the diagrams on p. 158 indicate that there was less physical opportunity for selection in winter although the nutritive quality of the individual components differed enormously. In contrast, when material of all ages was relatively highly digestible (May, June and July), sward structure was such that an animal would have removed the best from it simply by grazing the top layer.

The simulation of patchy grazing and the avoidance of excreta requires the introduction of a horizontal dimension to the pasture model. This could be achieved by producing a grid map of the pasture and recording, very simply, the state of the pasture in

each section of the grid, e.g. whether or not it has been grazed, how severely, and whether or not it has been contaminated by dung and urine. The size of the grid cells would need to correspond to the size of the pattern being investigated, e.g. MORRIS's patches (1967) of 16 cm × 16 cm (see p. 67); the area contaminated by a dung pat or urine patch; or the area covered by groups of sheep belonging to breeds which tend to graze close to one another (SPEDDING, 1965).

In the model, grazing takes place from the sward structure (compartment G, Fig. 6.1, p. 240) for the duration of the time step that is being used, e.g. 4 days. At the end of the 4 days, the structure of the defoliated sward (compartment J) is made to affect its subsequent growth and form: for instance, if defoliation were severe then the weight of subsequent fully emerged leaves (compartment K_2) would be reduced (see p. 268). If the model were modified so that a variable percentage of tillers within a group (i.e. a "plant") could be grazed at one time, then the weight of regrowth might be further expressed as a function of the percentage of tillers within a "plant" that had been left intact (Lit. Rev. p. 78 and p. 83).

Severity of defoliation, removal of reproductive apices, and trampling would have their effects on tiller production and death (compartment H).

The material left after grazing would automatically determine the weight of older leaves passing into the litter layer (compartment D).

The structure of the tiller after grazing would be carried over into the updated vertical distribution of dry matter (compartment C).

6.7 FURTHER DEVELOPMENT OF THE PASTURE MODEL

The conceptual model is ready to be coded into a computer program; some of the quantitative relationships required for it have been derived in this Chapter. Quantitative information on some components, however, is inadequate.

In the pasture model, as in the field, the addition of new material to the growing tiller, and the disappearance of dead material out of the litter layer, are crucial components determining the weight of dry matter above ground level. The important contribution made by reproductive tillers to gross crop growth rate, and yet the relative lack of information on the rate of development of the individual parts except in Timothy (I. DAVIES, 1969) have already been pointed out (p. 279).

Very little information is available on the disappearance of dead herbage from pasture, although a build-up of litter in the field may have a deleterious effect both on pasture production (by restricting tiller bud development, Lit. Rev., p. 82) and on animal production by lowering the mean digestibility of ingested material (Fig. 4.3.14, p. 137). Passage of material through the litter layer will require considerably more attention in the representation of pasture.

The essential output of a pasture model for grazing studies is the vertical distribution of material. While there is information available on leaf weight and weight per unit length, there is little on leaf angle and none on leaf curvature. The amount of detail required on the components of the model, such as leaf angle and leaf curvature, will become apparent from the results that the model produces.

The task of modelling an agricultural production system can appear overwhelming. However, except as an intellectual exercise, it is not the function of a model to encompass the whole detail of a system but rather to incorporate those components necessary for the exploration of particular questions about the system. The questions asked of the model will determine the level of detail put into its further development. As part of a larger grazing systems model, the pertinent questions will be the degree of pasture utilization, the regrowth produced afterwards, and the intake of the animal. If factors influencing regrowth were being examined in detail, then particular attention would be paid to the carbon metabolism of the plant. If, on the other hand, the mechanics of grazing were being considered, then more attention would be focussed on the spatial distribution of dry matter.

The purpose of a grazing systems model is not only to provide a tool for developing pasture production systems. It also acts as a framework of communication between specialists working on particular components of the system, and points to parameters on which information is needed to relate intake and sward structure. It is hoped that this conceptual model of pasture structure will contribute to the modelling of grazed pasture by other bodies.

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APPENDIX 1

CHEMICAL COMPONENTS AND APPARENT DIGESTIBILITIES OF PERENNIAL RYEGRASS (var. S24 unless otherwise stated)

	LEAF BLADE		LEAF SHEATH		YOUNG STEM		WHOLE PLANT (early reproductive)		MATURE STEM		Source of Information
	% CONTENT	% APP. DIG.	% CONTENT	% APP. DIG.	% CONTENT	% APP. DIG.	% CONTENT	% APP. DIG.	% CONTENT	% APP. DIG.	
CELL CONTENTS											
Ether soluble (Lipids, pigments, waxes)	approx. 10%	*45-70*	approx. 10%	*45-70*			8.5	*66*			(a) (d)
Water soluble carbohydrates		*100*				*100*		*100*		*100*	(a) (b) (c) (d)
Hexoses	1-2				3-7**		2-5		4-6**		
Sucrose	2-6				1-5**		5-7 } 13-24		2-4**		
Fructosan	0-6				4-14**		4-15		15-21**		
Organic acids	4*	*94*					4	*94*			(a)
Crude Protein											
Protein N × 6.25	} 27-11	*79*	} 15†-8	*79*	} 6,17-19**		15 } 21-11	*84*	3,9-6**	*24*	(a) to (g)
Nonprotein N × 6.25							3	*66 80*			
SUB-TOTAL	66								49		(b)
CELL WALL CONSTITUENTS											
Cellulose	16-25	*97-80*	25	*82*	24**		14-24	*94-65†*	22,25-27**	*61*	(a) (b) (c) (d) (f) (h) (i) (j)
Hemicelluloses											
Xylan	6-11	*89*	15		7-12**		7-9	*92-86*	16,12-13**		
Araban	2-3	*95*	3		2-3**		1-4	*95*	2,3**		
Glucan	2* } 16	*96*	3 } 23				2-3 } 12-17	*93* } *88*	2 } 20	} *56*	(a) (b) (c) (d)
Galactan	1	*94*			1*		0.5	*94*	0.8**		
Aldobiuronics	4*	*89*					4	*70*			
Pectin	2*	*72*					2-3	*71*	2	*36**	(a) (c) (k)
Lignin	2†-5		1†-5		1-5		3	*87-42*	6**,8	*0**	(a) (b) (c) (d) (e) (f) (k)
SUB-TOTAL	34								51		(b)
Ash (silica-free)							7				
Silica							0.5 } 7-12	*60*			(a) (c)
ORGANIC MATTER DIGESTIBILITY OF PLANT PART	*83-65*		*87-67-41*		*85-77*		*88-78*		*77-45*		(a) (c) (d) (e) (ℓ)

* S23 † Grasslands Ruanni ** STEM PLUS SHEATH (reference (b))

Table compiled from
(a) WAITE, JOHNSTON & ARMSTRONG (1964);
(b) MACKENZIE & WYLAM (1957);
(c) WAITE (1970);
(d) JARRIGE & MINSON (1964);
(e) JOHNSTON & WAITE (1965);
(f) WILKINS (1972);
(g) TILLEY & TERRY (1969);
(h) WILKINS & MINSON (1970)†;
(i) TILLEY, TERRY, DERIAZ & OUTEN (1969);
(j) JARRIGE (1963)*;
(k) WAITE, JOHNSTON & ARMSTRONG (1962)*;
(ℓ) TERRY & TILLEY (1964)

APPENDIX 2 The relationship of different parts of the grass plant to the movement of assimilates and minerals, in S24 ryegrass

PLANT PART	ACTIVITY	RESPIRATION	IMPORT					EXPORT					MINERAL MOVEMENT		ORDER OF PRIORITY OVER RESOURCES
		% of current assimilate respired within 24 hr. (c)	% import of current assimilate in whole plant after allowing for respiration losses	Proportion derived from each leaf: 1st leaf (c)	2nd leaf (c)	3rd leaf (c)	4th leaf (c)	% export of assimilate produced in that leaf †	Proportion of export that goes to each main sink in a vegetative tiller: terminal meristem	older leaves	roots	tillers	IMPORT	EXPORT	(e)
TERMINAL VEGETATIVE MERISTEM	Production of leaf initials.		17-31% (a) (b) (c)	0.58	0.25	0.13	0.04	0%					✓✓		1(ii)
	Expanding portion of first leaf.														2
1st LEAF	Expanded portion, photosynthesising.	16%						74%	0.79		0.05	0.15			None
2nd LEAF	Youngest fully expanded leaf, photosynthesising. Largest source of current assimilate.	28%						60%	0.30 (c) 0.20-0.25 (b) 0.32 (a)	0.02	0.21	0.46 0.20-0.30 (a)			None
3rd LEAF	Photosynthesising at a lower rate, and beginning to senesce. Substantial export of mobile mineral elements.	27%						63%	0.19		0.23	0.56		✓✓	None
4th LEAF	Senescing or dead. Perhaps some export of mobile mineral elements.	35%						52%	0.12		0.30	0.57		✓	None
VEGETATIVE STEM			1.5 - (c) 3.0% (a)												
ADJACENT TILLERS	Become increasingly independent of main tiller for assimilates.		33% (c) 10-26% (b)	0.10	0.35	0.38	0.17	Some export to parent tiller and other daughter tillers.							5
ROOTS	Water and mineral uptake; anchorage.		14% (c) but ranges widely	0.07	0.36	0.36	0.21	0%						✓✓	4
TERMINAL REPRODUCTIVE MERISTEM			22%, (a) increasing rapidly to 66% as ear emerges from flag leaf.										✓✓		1(i)
REPRODUCTIVE STEM			3% (a) (initially) to 52% (stem elongation) to 20% (flag leaf expansion) at expense of tillers and roots.												3

† calculated from RYLE & POWELL 1974

% current assimilate produced by leaf in 24 hrs = 100%
% lost by respiration in 24 hrs = RL%
∴ % remaining in plant after respiration losses (24 hrs) = 100 - RL%
% of above exported from fed leaf in 24 hrs = E%
∴ % of assimilate produced by leaf that is exported within 24 hrs = E% × (100 - RL)%

Sources:

(a) RYLE 1970a.
(b) RYLE 1970b.
(c) RYLE & POWELL, 1974.
(d) MARSHALL & SAGAR, 1968 (*L. multiflorum*).
(e) BEGG & WRIGHT, 1964 (*Phalaris arundinacea*)

APPENDIX 3 SWARD MANAGEMENT AND SAMPLING DATES

April

3.4.74 COMPOUND FERTILIZER, 250 Kg ha^{-1} of 29-5-5 (73 Kg N ha^{-1}, 12.5 Kg P ha^{-1}, 12.5 Kg K ha^{-1}).

May

3.5.74 Preliminary measurements on sward structure and digestibility.

4.5.74 FIELD CUT TO 4 CM.

6.5.74 FERTILIZER, Nitram, applied, N1 = 0, N2 = 67, N3 = 134, N4 = 202 Kg N ha^{-1}

7.5.74 Yield of surrounding area measured.

9-10.5.74 Put rings on tillers to be used for permanent observation.

11.5.74 Started age structure records of N2, N3, N4.

14.5.74 Determined soluble nitrogen content of the soil.

24.5.74 Heights and digestibilities of tiller parts sampled.

25.5.74 PLOTS CUT TO 4 CM.

June

11.6.74 Started age structure records of N1.

12.6.74 Determined soluble nitrogen content of the soil.

22-27.6.74 Yield, sward structure and digestibility sampling.

28.6.74 PLOTS CUT TO 4 CM.

July

23.7.74 Determined soluble nitrogen content of the soil.

August

12-16.8.74 Yield, sward structure and digestibility sampling.

20.8.74 PLOTS CUT TO 4 CM.

23.8.74 FERTILIZER, Nitram, applied, N1 = 23, N2 = 45, N3 = 67, N4 = 90 Kg N ha^{-1}

September

9.9.74 Determined soluble nitrogen content of the soil.

October

30.9.74
-4.10.74 Yield, sward structure and digestibility sampling.

9.10.74 Samples taken from N1 and N4 for water-soluble carbohydrates and Van Soest snalysis.

November

6.11.74 Yield and digestibility sampling.

7-8.11.74 PLOTS CUT TO 4 CM.

December

16.12.74 Digestibility and weight sampling.

January

16-20. 1.75 Yield, sward structure and digestibility sampling. (N1 and N4)

March

3 - 5. 3.75 Yield, sward structure and digestibility sampling. (N1 and N4)

April

2 - 4. 4.75 Digestibility and sward structure sampling. (N1 and N4)

5,7,9.4.75 Yield (N1 and N4)

17.4.75 COMPOUND FERTILIZER, 250 Kg ha^{-1} of 29-5-5 (73 Kg N ha^{-1}, 12.5 Kg P ha^{-1}, 12.5 Kg K ha^{-1}).

25.4.75 Determined soluble nitrogen content of the soil.

May

4 - 7. 5.75 Yield, sward structure and digestibility sampling. (N1 and N4)

15.5.75 PLOTS CUT TO 4 CM, except N3 (left uncut).

16.5.75 FERTILIZER, Nitram, applied,

N1 = 0, N2 = 67, N4 = 202 Kg N ha^{-1}

21.5.75 Sward structure and digestibility of reproductive tillers.

26.5.75 Sward structure and digestibility of reproductive tillers.

29.5.75 Determined soluble nitrogen content of the soil.

June

3.6.75 Sward structure and digestibility of reproductive tillers.

4-7.6.75 Sward structure and digestibility sampling (N1, N2, N4).

7-8.6.75 Yield of all plots.

20.6.75 Determined soluble nitrogen content of the soil.

July

1-5.7.75 Sward structure and digestibility sampling of vegetative and reproductive tillers.

6-7.7.75 Yield of all plots.

12.7.75 Determined soluble nitrogen content of the soil.

APPENDIX 4 ; Chart showing Week Number (boxed) in relation to Calendar Date.

JAN 1	29	26	26	23	21	18	16	13	10	8	5	3
2	30	27	27	24	22	19	17	14	11	9	6	4
3	31 JAN	28 FEB	28	25	23	20	18	15	12	10	7	5
4	FEB 1	MAR 1	29	26	24	21	19	16	13	11	8	6
5	2	2	30	27	25	22	20	17	14	12	9	7
6	3	3	31 MAR	28	26	23	21	18	15	13	10	8
7 [1]	4 [5]	4 [9]	APR 1 [13]	29 [17]	27 [21]	24 [25]	22 [29]	19 [33]	16 [37]	14 [41]	11 [45]	9 [49]
8	5	5	2	30 APR	28	25	23	20	17	15	12	10
9	6	6	3	MAY 1	29	26	24	21	18	16	13	11
10	7	7	4	2	30	27	25	22	19	17	14	12
11	8	8	5	3	31 MAY	28	26	23	20	18	15	13
12	9	9	6	4	JUN 1	29	27	24	21	19	16	14
13	10	10	7	5	2	30 JUN	28	25	22	20	17	15
14 [2]	11 [6]	11 [10]	8 [14]	6 [18]	3 [22]	JUL 1 [26]	29 [30]	26 [34]	23 [38]	21 [42]	18 [46]	16 [50]
15	12	12	9	7	4	2	30	27	24	22	19	17
16	13	13	10	8	5	3	31 JUL	28	25	23	20	18
17	14	14	11	9	6	4	AUG 1	29	26	24	21	19
18	15	15	12	10	7	5	2	30	27	25	22	20
19	16	16	13	11	8	6	3	31 AUG	28	26	23	21
20	17	17	14	12	9	7	4	SEP 1	29	27	24	22
21 [3]	18 [7]	18 [11]	15 [15]	13 [19]	10 [23]	8 [27]	5 [31]	2 [35]	30SEP [39]	28 [43]	25 [47]	23 [51]
22	19	19	16	14	11	9	6	3	OCT 1	29	26	24
23	20	20	17	15	12	10	7	4	2	30	27	25
24	21	21	18	16	13	11	8	5	3	31 OCT	28	26
25	22	22	19	17	14	12	9	6	4	NOV 1	29	27
26	23	23	20	18	15	13	10	7	5	2	30 NOV	28
27	24	24	21	19	16	14	11	8	6	3	DEC 1	29
28 [4]	25 [8]	25 [12]	22 [16]	20 [20]	17 [24]	15 [28]	12 [32]	9 [36]	7 [40]	4 [44]	2 [48]	30 [52]
												31 DEC

APPENDIX 5 : Ages of leaves at leaf positions 1 to 4, in days.
S.E. given in italics. Vegetative tillers.

WEEK 1974	N LEVEL	LEAF POSITION 1		2		3		4	
22	2	7	*0.5*	17	*0.5*				
23	2	6	*0.5*	19	*0.6*				
24	2	7	*0.5*	20	*0.7*	29	*0.7*		
25	1	8	*0.4*						
	2	9	*0.6*	22	*0.7*	34	*0.7*		
24. 6.74	3	7	*0.6*	18	*0.7*	30	*0.9*	37	*1.0*
	4	7	*0.5*	17	*0.6*	27	*0.9*	37	*1.0*
26	2	11	*0.7*	25	*0.7*	37	*0.8*	45	*0.6*
27	1	6	*0.5*	23	*0.4*				
28	1	9	*0.5*	26	*0.8*				
29	1	9	*0.7*	24	*1.0*	35	*0.8*		
30	1	8	*0.7*	25	*0.9*	39	*1.1*		
31	1	7	*0.6*	24	*1.0*	39	*1.3*	50	*1.0*
32	1	8	*0.5*	24	*0.9*	41	*1.3*	53	*1.4*
33	1	6	*0.5*	22	*0.7*	38	*1.1*	53	*1.4*
	2	7	*0.5*	25	*0.8*	43	*1.2*	60	*1.6*
14. 8.74	3	7	*0.5*	25	*0.7*	42	*1.0*	57	*1.5*
	4	9	*0.6*	26	*0.8*	42	*0.8*	53	*1.4*
34	1	7	*0.5*	23	*0.6*	38	*1.0*	54	*1.5*
35	1	6	*0.5*	21	*0.8*	37	*1.1*	52	*1.6*
36	1	7	*0.4*	20	*0.7*	36	*0.9*	51	*1.3*
37	1	9	*0.5*	22	*0.6*	38	*0.9*	53	*1.2*
38	1	10	*0.7*	24	*0.6*	38	*1.0*	53	*1.3*
39	1	14	*0.7*	29	*0.5*	43	*0.9*	59	*1.2*
	2	13	*0.7*	29	*0.6*	41	*1.0*	56	*1.4*
2.10.74	3	13	*0.5*	26	*0.5*	37	*0.7*	52	*1.2*
	4	13	*0.5*	26	*0.4*	37	*0.6*	53	*1.1*
40	1	18	*0.8*	35	*0.5*	48	*0.9*	64	*1.2*
41	1	17	*1.1*	38	*0.6*	51	*0.8*	66	*1.2*
42	1	19	*1.2*	43	*0.7*	56	*0.9*	71	*1.4*
43	1	22	*1.4*	47	*0.9*	62	*0.9*	76	*1.5*
44	1	23	*1.5*	52	*0.9*	67	*0.9*	81	*1.4*
	2	25	*1.4*	53	*0.7*	66	*0.7*	79	*1.2*
6.11.74	3	21	*1.2*	50	*0.6*	63	*0.5*	73	*1.0*
	4	20	*1.2*	48	*0.7*	62	*0.5*	72	*0.8*
45	1	27	*1.6*	58	*1.0*	74	*0.9*	88	*1.5*
46	1	23	*1.9*	59	*1.4*	77	*0.9*	90	*1.3*
47	1	26	*1.9*	63	*1.6*	81	*0.9*	95	*1.4*
48	1	27	*2.0*	65	*1.8*	87	*0.9*	100	*1.1*
49	1	28	*2.2*	68	*2.1*	92	*1.2*	106	*1.2*
	2	31	*2.0*	73	*1.9*	93	*1.2*	106	*1.3*
16.12.74	3	29	*2.1*	68	*2.2*	89	*1.1*	100	*1.0*
	4	31	*1.7*	69	*1.6*	90	*0.9*	101	*0.9*
50	1	27	*2.1*	69	*2.4*	96	*1.6*	111	*1.3*
51	1	31	*2.1*	73	*2.4*	101	*1.7*	117	*1.4*
52	1	26	*2.4*	71	*2.8*	104	*2.2*	121	*1.6*

APPENDIX 5 cont. : Ages of leaves at leaf positions 1 to 4, in days.

S.E. given in italics. Vegetative tillers.

WEEK 1975	N LEVEL	LEAF POSITION 1		2		3		4	
1	1	26	*2.5*	74	*2.8*	110	*2.1*	127	*1.6*
2	1	18	*2.1*	68	*2.9*	105	*3.1*	127	*1.6*
3	1	21	*2.2*	70	*3.2*	109	*3.4*	133	*1.9*
	2	26	*3.4*	75	*4.1*	118	*4.1*	137	*2.7*
18. 1.75	3	20	*1.5*	71	*2.4*	113	*2.3*	132	*1.1*
	4	23	*3.3*	71	*3.8*	111	*3.1*	132	*1.5*
4	1	25	*2.1*	73	*3.1*	114	*3.6*	139	*2.1*
5	1	28	*2.3*	76	*3.5*	115	*4.1*	144	*2.4*
6	1	34	*2.3*	82	*3.5*	121	*4.0*	151	*2.4*
7	1	32	*2.8*	79	*3.5*	122	*3.7*	154	*2.5*
8	1	32	*2.8*	79	*3.3*	125	*3.5*	160	*2.5*
9	1	27	*3.3*	77	*3.6*	124	*4.2*	162	*4.0*
	2	25	*2.8*	81	*4.2*	126	*5.2*	165	*4.0*
4. 3.75	3	20	*2.5*	67	*2.9*	112	*3.5*	159	*3.6*
	4	24	*3.4*	71	*3.8*	121	*4.5*	159	*3.6*
10	1	24	*3.0*	76	*3.3*	123	*4.2*	162	*4.3*
11	1	24	*2.9*	76	*3.4*	122	*4.0*	163	*4.4*
12	1	24	*3.0*	74	*3.9*	119	*4.4*	160	*4.7*
13	1	20	*2.9*	68	*4.1*	117	*4.5*	159	*4.8*
14	1	19	*3.0*	65	*4.2*	113	*4.2*	157	*4.7*
	2	20	*2.4*	69	*4.2*	119	*5.4*	164	*6.6*
4. 4.75	3	15	*1.7*	54	*2.7*	98	*3.0*	146	*4.2*
	4	26	*3.6*	69	*5.7*	118	*6.4*	162	*5.5*
15	1	20	*3.1*	63	*4.2*	113	*4.3*	158	*4.9*
16	1	14	*3.4*	50	*5.2*	95	*6.0*	139	*6.1*
17	1	4	*0.5*	18	*2.1*	53	*4.6*	95	*6.0*
18	1	7	*0.6*	19	*1.9*	43	*4.1*	83	*5.1*
	2	9	*1.2*	22	*2.0*	54	*4.1*	100	*6.2*
4. 5.75	3	8	*0.6*	23	*1.4*	54	*2.4*	93	*3.3*
	4	5	*0.8*	22	*4.9*	47	*8.1*	84	*10.9*
19	1	12	*0.9*	24	*1.7*	47	*3.6*	86	*4.5*
20	1	9	*2.6*						
21	1	3	*0.5*	22	*3.6*				
22	1	6	*0.4*	19	*1.5*	36	*11.5*		
	2	6	*0.3*	19	*1.3*				
4. 6.75	4	6	*0.5*	21	*1.7*	30	*3.6*	48	*6.6*
23	1	6	*0.5*	16	*0.6*				
24	1	8	*0.6*	19	*0.5*	27	*1.3*		
25	1	8	*0.6*	22	*0.6*	30	*0.8*		
26	1	10	*0.7*	25	*0.7*	35	*0.8*	44	*2.6*
	2	10	*0.7*	23	*0.7*	31	*0.9*	39	*2.6*
	4	9	*0.7*	20	*0.5*	28	*0.7*	34	*1.0*

APPENDIX 6 Dry weights of parts of the vegetative tiller, mg. (S.E. given in italics).

Sampling Date	Treatment	1L	2B	2S	3B	3S	4B	4L	4S	Litter	Total including litter	Total excluding litter
Fertilizer treatments applied 6.5.74												
24. 6.74	N1	6.52 *0.38*	9.37 *0.58*	2.83 *0.11*		2.64 *0.16*				9.30 *0.34*	32.75 *1.02*	23.45 *0.74*
	N2	6.51 *0.19*	9.09 *0.22*	2.61 *0.68*		2.29 *0.15*				7.70 *0.63*	32.79 *0.64*	24.51 *0.22*
	N3	6.79 *0.73*	9.39 *0.91*	4.47 *0.20*		2.76 *0.30*				7.67 *0.83*	33.42 *2.71*	25.74 *2.67*
	N4	6.56 *0.24*	8.34 *0.36*	4.30 *0.22*		2.57 *0.06*				6.20 *1.01*	30.96 *1.71*	24.75 *1.74*
14. 8.74	N1	5.00 *0.79*	7.75 *0.26*	3.33 *0.32*	9.25 *0.54*	2.79 *0.23*		10.10 *0.36*		13.63 *1.55*	45.32 *4.41*	31.67 *4.00*
	N2	4.46 *0.44*	7.36 *0.14*	2.96 *0.27*	7.54 *0.26*	2.48 *0.02*		8.63 *0.42*		15.40 *2.88*	42.28 *0.88*	26.08 *5.67*
	N3	5.79 *0.66*	10.29 *0.76*	3.92 *0.35*	9.99 *0.60*	3.84 *0.10*		11.46 *3.25*		12.84 *2.76*	46.91 *2.80*	34.08 *1.39*
	N4	6.11 *0.64*	10.59 *1.37*	4.14 *0.25*	10.57 *2.51*	4.37 *0.29*		9.77 *2.40*		10.64 *1.13*	45.68 *3.24*	35.05 *4.28*
Fertilizer treatments applied 23.8.74												
2.10.74	N1	4.94 *0.15*	7.64 *0.59*	2.74 *0.11*	6.01 *0.17*	2.69 *0.11*		8.26 -		7.27 *0.90*	32.02 *2.15*	23.45 *1.84*
	N2	5.59 *0.21*	8.45 *0.86*	3.18 *0.16*	5.92 *0.18*	2.80 *0.24*		9.82 -		6.80 *0.45*	30.12 *2.26*	23.32 *2.28*
	N3	5.41 *0.68*	8.83 *0.58*	3.26 *0.24*	7.60 *0.36*	2.77 *0.13*				3.38 *0.37*	28.03 *1.81*	24.65 *1.52*
	N4	6.57 *0.35*	8.37 *0.54*	3.36 *0.22*	6.65 *0.25*	2.43 *0.24*				4.74 *1.64*	29.72 *3.74*	26.02 *1.60*
17. 1.75	N1	1.95 *0.04*	3.63 *0.26*	0.92 *0.04*	3.40 *0.28*	1.66 *0.17*		11.62 *1.75*		11.19 *0.62*	23.09 *0.11*	11.90 *0.73*
	N4	1.59 *0.11*	2.90 *0.14*	0.94 *0.08*	3.12 *0.12*	2.45 *0.17*				9.02 *1.75*	17.80 *1.82*	8.77 *0.29*
4. 3.75	N1	1.89 *0.14*	4.49 *0.63*	1.17 *0.21*	4.00 *1.15*	1.00 *0.08*		6.55 *0.97*		9.28 *1.24*	20.81 *2.29*	11.53 *1.06*
	N4	1.98 *0.04*	4.44 *0.38*	1.27 *0.02*	5.73 *0.73*	1.42 *0.18*		9.15 *2.14*		5.14 *0.74*	17.18 *0.79*	12.04 *0.69*
4. 4.75	N1	2.27 *0.07*	5.10 *0.23*	1.56 *0.04*	4.20 *0.52*	1.48 *0.16*				10.33 *1.37*	27.52 *2.40*	17.19 *1.13*
	N4	2.23 *0.13*	4.31 *0.22*	1.53 *0.15*	3.94 *0.60*	1.17 *0.05*				5.37 *0.84*	20.40 *1.23*	15.04 *0.81*
4. 5.75	N1	3.18 *0.39*	5.35 *0.34*	1.40 *0.11*	3.04 *0.09*	1.00 *0.07*		2.84 *0.20*		7.18 *2.37*	21.47 *2.60*	14.29 *0.71*
	N4	3.29 *0.35*	5.56 *0.32*	1.79 *0.28*	3.03 *0.26*	1.36 *0.18*		3.37 *0.31*		7.06 *0.76*	24.28 *0.97*	17.71 *1.97*
Fertilizer treatments applied 16.5.75												
4. 6.75	N1	3.85 *0.53*	7.23 *1.08*	1.72 *0.32*	3.39 *0.73*	1.38 *0.12*	2.12 *0.28*		2.12 *1.02*	2.09 *0.25*	19.43 *2.22*	17.35 *2.36*
	N2	4.14 *0.73*	6.96 *0.84*	1.73 *0.33*	3.71 *0.37*	1.34 *0.17*	1.88 *0.17*		1.96 *0.52*	2.80 *0.65*	20.25 *2.11*	17.46 *2.60*
	N4	4.09 *0.54*	5.91 *0.60*	1.50 *0.19*	3.73 *0.49*	1.16 *0.10*	1.79 *0.17*		2.45 *0.95*	2.06 *0.27*	17.23 *1.92*	15.17 *2.09*
4. 7.75	N1	5.84 *0.35*	11.57 *0.43*	2.77 *0.38*	8.23 *0.08*	2.24 *0.22*		6.46 *1.07*		3.05 *0.54*	37.46 *1.73*	34.41 *1.22*
	N2	7.86 *0.19*	12.45 *0.72*	4.70 *0.50*	6.91 *0.41*	2.40 *0.31*		3.75 *0.48*		1.96 *0.65*	37.89 *2.85*	35.93 *2.24*
	N4	7.49 *1.02*	10.54 *1.40*	3.60 *0.44*	5.38 *0.73*	2.04 *0.39*		3.16 *0.34*		2.57 *0.08*	32.32 *4.08*	29.76 *4.07*

APPENDIX 7 Lowest and highest points, and ligule height, of leaf blades 1 to 4. Vegetative tillers. S.E.'s are given in italics.

Sampling Date	Treatment	1st Leaf, mm		2nd Blade, mm			3rd Blade, mm			4th Blade, mm		
		Height of Emergence	Max	Min	Max	Ligule	Min	Max	Ligule	Min	Max	Ligule
Fertilizer treatments applied 6.5.74												
24. 6.74	N1	24 *1.2*	84 *2.9*	24 *1.2*	113 *2.7*	24 *1.2*	20 *0.7*	81 *4.0*	20 *0.7*			
	N2	31 *0.9*	99 *3.4*	31 *0.8*	135 *1.6*	31 *0.8*	24 *0.9*	92 *4.1*	25 *0.8*			
	N3	42 *1.4*	129 *4.5*	46 *1.1*	171 *4.3*	46 *1.1*	35 *1.1*	125 *5.0*	35 *1.0*			
	N4	54 *2.1*	148 *4.8*	57 *1.6*	195 *5.4*	57 *1.6*	39 *1.4*	133 *5.4*	39 *1.4*	31 *3.4*	97 *14.5*	31 *3.4*
15. 8.74	N1	19 *0.5*	61 *1.8*	19 *0.5*	85 *2.1*	19 *0.5*	17 *0.6*	88 *2.6*	18 *0.6*	17 *0.9*	84 *4.1*	18 *0.8*
	N2	20 *0.6*	63 *2.1*	20 *0.6*	93 *1.8*	20 *0.6*	20 *0.9*	90 *2.8*	20 *0.9*	20 *1.3*	75 *4.5*	20 *1.2*
	N3	26 *0.8*	75 *2.4*	26 *0.8*	116 *2.6*	26 *0.8*	25 *0.8*	109 *3.2*	25 *0.8*	26 *1.7*	94 *5.9*	27 *1.5*
	N4	25 *0.7*	72 *2.3*	25 *0.7*	108 *2.9*	25 *0.7*	25 *0.9*	105 *3.8*	26 *0.8*	26 *1.4*	97 *5.5*	27 *1.2*
Fertilizer treatments applied 23.8.74												
2.10.74	N1	19 *0.5*	59 *2.3*	19 *0.5*	83 *2.6*	19 *0.5*	16 *0.7*	61 *3.1*	16 *0.7*	12 *0.8*	42 *2.4*	12 *0.7*
	N2	21 *0.8*	67 *2.5*	23 *0.7*	105 *3.0*	23 *0.7*	20 *0.8*	80 *3.9*	21 *0.8*	18 *1.1*	60 *4.4*	18 *1.1*
	N3	25 *0.9*	79 *2.9*	27 *0.8*	124 *3.7*	27 *0.8*	24 *0.8*	92 *4.1*	24 *0.8*	19 *1.2*	74 *4.9*	19 *1.2*
	N4	31 *0.8*	98 *3.7*	31 *0.8*	129 *3.7*	31 *3.7*	24 *0.9*	96 *4.1*	25 *0.9*	18 *0.9*	60 *4.1*	18 *0.9*
17. 1.75	N1	14 *0.5*	33 *1.2*	14 *0.5*	40 *1.5*	15 *0.5*	14 *0.6*	27 *1.1*	15 *0.6*	18 *1.5*	32 *5.2*	20 *1.4*
	N4	20 *0.5*	39 *1.3*	19 *0.6*	40 *1.5*	19 *0.5*	19 *1.0*	29 *1.6*	21 *0.8*			
4. 3.75	N1	14 *0.4*	32 *1.2*	13 *0.5*	46 *1.6*	14 *0.4*	11 *0.6*	36 *3.9*	14 *0.5*	14 *2.7*	31 *7.3*	15 *1.1*
	N4	16 *0.5*	38 *1.4*	15 *0.6*	45 *1.8*	16 *0.5*	15 *1.0*	34 *2.6*	17 *0.7*			17 *1.5*
3. 4.75	N1	13 *0.5*	31 *1.2*	13 *0.5*	47 *1.3*	13 *0.5*	11 *0.5*	32 *1.6*	12 *0.4*	11 *0.7*	24 *1.7*	12 *0.4*
	N4	15 *0.4*	36 *1.3*	14 *0.4*	50 *1.5*	15 *0.4*	11 *0.5*	30 *1.4*	13 *0.4*	11 *0.7*	20 *1.4*	14 *0.5*
6. 5.75	N1	21 *0.8*	68 *2.5*	21 *0.8*	95 *3.2*	21 *0.8*	14 *0.8*	49 *1.9*	15 *0.8*	7 *0.6*	30 *2.1*	7 *0.5*
	N4	26 *1.0*	71 *2.6*	26 *1.0*	107 *3.2*	26 *1.0*	20 *1.1*	58 *2.5*	21 *1.1*	10 *0.9*	37 *2.1*	11 *0.7*
Fertilizer treatments applied 16.5.75												
6. 6.75	N1	23 *0.6*	70 *2.7*	23 *0.6*	109 *3.1*	23 *0.6*	18 *0.7*	54 *2.8*	19 *0.7*	15 *1.4*	33 *2.4*	16 *1.4*
	N2	27 *0.8*	78 *3.1*	27 *0.8*	117 *3.3*	27 *0.8*	19 *0.9*	60 *3.3*	21 *0.7*	16 *1.8*	31 *3.0*	18 *1.7*
	N4	27 *0.9*	82 *3.3*	27 *0.9*	110 *3.9*	27 *0.9*	19 *1.0*	66 *4.7*	19 *1.0*	21 *2.9*	39 *4.7*	23 *2.4*
3. 7.75	N1	20 *0.7*	69 *3.1*	20 *0.7*	128 *3.0*	20 *0.7*	17 *0.7*	103 *3.4*	18 *0.6*	14 *0.7*	69 *4.2*	15 *0.7*
	N2	38 *1.1*	119 *4.6*	38 *1.1*	194 *4.5*	38 *1.1*	28 *1.2*	127 *5.3*	29 *1.1*	18 *1.2*	77 *5.0*	19 *1.1*
	N4	61 *1.7*	163 *5.8*	61 *1.7*	244 *5.9*	61 *1.7*	39 *1.9*	140 *6.3*	40 *1.8*	18 *1.4*	70 *5.1*	20 *1.2*

APPENDIX 8 : *In Vitro* Organic Matter Digestibilities of plant parts. Vegetative tillers.

S.E. of three replicates given in italics.

Date	N Level	1L	2B	2S	3B	3S	4L	Loose Litter	Whole plant + Litter
24. 6.74	1	86.0 *0.8*	85.7 *0.6*	89.1	82.2 *0.4*	86.0		61.5 *0.8*	
	2	85.4 *1.7*	85.6 *0.8*	88.6	83.8 *0.9*	83.8		57.5 *1.1*	
	3	83.2 *1.1*	84.4 *0.8*	88.2	81.9 *1.1*	84.5		56.1 *0.6*	
	4	81.9 *0.4*	82.1 *0.2*	87.5	81.1 *0.8*	84.6		56.3 *0.3*	
14. 8.74	1	92.2 *0.7*	90.4 *0.5*	93.6 *0.3*	82.8 *0.4*	91.2 *1.2*	78.7 *1.5*	51.8 *1.7*	
	2	92.4 *0.8*	88.9 *1.6*	91.7 *1.5*	82.7 *2.1*	91.4 *1.1*	77.2 *3.5*	52.2 *5.8*	
	3	92.2 *0.7*	88.9 *1.3*	92.6 *1.1*	82.6 *1.2*	88.7 *1.9*	75.1 *4.1*	52.4 *5.8*	
	4	91.9 *0.4*	86.8 *1.0*	93.1 *1.3*	82.5 *2.0*	87.0 *2.2*	71.6 -	46.1 *3.6*	
2.10.74	1	91.9 *0.3*	88.3 *0.4*	93.4 *0.6*	83.1 *0.1*	86.2 *1.3*	64.9 *1.8*	42.6 *1.1*	
	2	91.0 *0.9*	88.1 *0.3*	92.1 *0.6*	83.5 *0.3*	86.9 *1.3*	67.1 *0.9*	44.6 *2.1*	
	3	90.4 *0.6*	86.9 *0.4*	93.0 *1.4*	81.8 *0.8*	85.2 *2.3*	66.5 *0.2*	40.5 *0.5*	
	4	89.2 *0.9*	86.6 *0.9*	91.2 *0.2*	82.4 *1.2*	84.7 *0.4*	66.1 *2.3*	41.3 *1.4*	
6.11.74	1	92.1	89.5	95.2	83.2	88.5	62.7	44.9	
	2	92.8	89.7	94.4	82.9	90.0	67.5	39.1	
	3	92.0	88.2	94.4	82.5	87.8	63.9	43.1	
	4	92.0	88.7	94.5	81.3	87.4	68.3	34.1	
17.12.74	1	90.2	86.8	91.4	73.8	80.9	60.2	37.1	59.0
	2	92.4	86.7	89.9	68.2	78.0	52.8	25.1	61.6
	3	89.7	85.5	87.7	66.1	78.4	59.1	38.3	65.0
	4	89.5	86.1	90.4	70.6	81.1	55.7	42.4	58.3

Cont...

APPENDIX 8 Cont. : *In Vitro* Organic Matter Digestibilities of plant parts. Vegetative tillers.

S.E. of three replicates given in italics.

Date	N Level	1L	2B	2S	3B	3S	4L	Loose Litter	Whole plant + Litter
18. 1.75	1	87.7 *1.6*	83.6 *0.8*	90.4	72.7 *1.4*	78.0 *1.0*	58.1 *1.4*	39.6 -	59.1 *1.2*
	4	88.9 *0.5*	83.5 *1.5*	88.5	72.5 *0.3*	75.4 -	62.3 *0.4*	41.2 *0.6*	58.1
4. 3.75	1	88.4 *0.3*	84.7 *0.5*	86.8 *0.2*	75.6 *0.6*	70.3 -	56.3 *1.4*	31.8 *1.6*	55.8 *3.1*
	4	87.8 *0.3*	84.3 *0.4*	85.7 *1.6*	73.8 *1.2*	71.1 -	51.5 *0.9*	31.4 *1.2*	55.5 *1.3*
4. 4.75	1	90.5 *0.5*	89.1 *0.5*	83.1 *0.4*	83.8 *0.5*	87.2 -	65.2 *1.3*		69.7 *2.7*
	4	89.6 *0.7*	87.5 *0.7*	91.9 *0.6*	82.3 *0.1*	82.6 *0.6*	58.8 *0.7*	37.7 *1.1*	69.8 *0.5*
4. 5.75	1	88.5 *0.8*	85.9 *0.8*	88.2 -	82.6 *1.8*	82.7 -	73.0 -		77.6 *1.6*
	4	89.5 *0.5*	85.3 *0.3*	88.7 -	82.5 *0.2*	80.3 -	72.8 -		82.9 *0.8*
4. 6.75	1	87.6 *0.8*	85.4 *0.6*	88.4 *0.9*	81.4 *0.2*			50.6 *2.2*	76.4 *2.0*
	2	86.8 *0.4*	85.1 *0.6*	87.6 *0.5*	81.6 *0.7*			46.4 *3.0*	76.9 *1.8*
	4	85.7 *0.2*	84.2 *0.3*	87.6 *0.3*	81.3 *0.7*			51.2 *3.2*	76.8 *1.7*
12. 6.75	1	88.2	86.9		83.2			} 54.2	
	4	85.4	84.0		83.3				
4. 7.75	1	77.3 *0.6*	77.4 *0.8*	76.5 *0.1*	77.7 *1.5*	76.3	72.3 *3.7*	61.2 -	74.7 *0.3*
	2	78.7 *0.7*	78.9 *0.1*	78.7 *0.5*	75.6 *1.0*	77.1	62.3 *0.9*	54.4 *3.7*	76.8 *0.4*
	4	83.4 *0.5*	78.2 *0.3*	82.3 *1.2*	74.7 *0.2*	75.0	62.3 -	53.9 *1.5*	77.3 *1.3*
22. 7.75	1	-	76.2		70.5		58.5		

APPENDIX 9 : Number of green leaves per tiller in Experiment 2, 3rd LI.

Green leaves are defined as being more than 50% green.

S.E. in italics.

GR	I	II	III	IV	V	VI	GR means
5°C	2.14	2.28	2.03	2.25	2.22	2.28	2.20
	0.08	*0.07*	*0.10*	*0.07*	*0.06*	*0.08*	
10°C	2.31	2.30	2.41	2.47	2.57	2.52	2.44
	0.09	*0.11*	*0.10*	*0.12*	*0.11*	*0.15*	
20°C	2.57	2.63	2.47	2.63	2.63	2.73	2.61
	0.13	*0.13*	*0.13*	*0.14*	*0.09*	*0.12*	
TR means	2.34	2.40	2.30	2.45	2.47	2.51	

Growth Room	Leaf Appearance Interval	1ST LEAF → 2ND BLADE							2ND BLADE → 3RD BLADE							3RD BLADE → 4TH LEAF						
		I	II	III	IV	V	VI	TR mean	I	II	III	IV	V	VI	TR mean	I	II	III	IV	V	VI	TR mean
5°C	0 - 1st	0.6	0.0	1.8	1.8	-1.0	1.0	0.7	6.4	10.8	8.0	16.6			10.4							
								0.44							*2.24*							
	1st - 2nd	3.6	4.8	1.4	1.6	4.8	3.6	3.3	11.8	14.8	7.4	15.6	9.2	8.0	11.1	25.8	26.2	24.6	26.0			25.6
								0.61							*1.43*							*0.36*
	2nd - 3rd	6.8	4.8	6.0	4.2	8.0	5.6	5.9	17.4	11.8	11.8	11.8	15.2	12.2	13.4	24.2	18.2	23.4	15.4	27.0	25.4	22.3
								0.56							*0.97*							*1.84*
10°C	0 - 1st	3.6	4.4	4.2	4.0	7.0	5.0	4.7	15.4	16.0	10.2	16.8	24.0	14.8	16.2							
								0.50							*1.83*							
	1st - 2nd	5.2	3.2	4.8	2.6	3.8	0.6	3.4	17.0	11.0	7.6	11.0	7.6	9.4	10.6	27.8	16.5	23.8	32.0	8.9	27.6	22.8
								0.68							*1.42*							*3.50*
	2nd - 3rd	5.4	7.0	3.6	5.6	4.6	2.6	4.8	14.8	11.8	10.6	17.2	9.2	12.8	12.7	16.4	22.0	17.8	30.0	17.6	20.8	20.8
								0.64							*1.19*							*2.04*
20°C	0 - 1st	5.8	1.4	1.6	1.6	3.6	0.4	2.4	9.2	8.4	7.6	11.2	4.8		8.2	17.0	20.0	16.8	16.6	9.2	24.0	17.3
								0.80							*1.05*							*1.99*
	1st - 2nd	3.8							0.6							3.4						
	2nd - 3rd	4.4							10.6							16.4						

Appendix 10 : Change in digestibility of a leaf as it ages. (IVOMD units). Experiment 2.

S.E. of the mean of the Treatments within one LI is given in italics.

GR	LI	1ST LEAF 2ND BLADE							2ND BLADE 3RD BLADE							3RD BLADE 4TH LEAF						
		I	II	III	IV	V	VI	TR mean	I	II	III	IV	V	VI	TR mean	I	II	III	IV	V	VI	TR mean
5°C	0 -1st	0.02	0.00	0.07	0.07	-0.04	0.04	0.03	0.25	0.43	0.32	0.64			0.41							
								0.017							*0.085*							
	1st-2nd	0.10	0.11	0.04	0.04	0.12	0.10	0.08	0.33	0.35	0.21	0.39	0.23	0.22	0.29	0.72	0.62	0.68	0.65			0.67
								0.015							*0.032*							*0.021*
	2nd-3rd	0.17	0.13	0.18	0.10	0.22	0.12	0.15	0.43	0.32	0.35	0.28	0.41	0.27	0.34	0.60	0.49	0.69	0.37	0.73	0.56	0.57
								0.018							*0.027*							*0.054*
10°C	0 -1st	0.14	0.19	0.16	0.14	0.28	0.18	0.18	0.62	0.70	0.38	0.60	0.96	0.53	0.63							
								0.021							*0.079*							
	1st-2nd	0.20	0.15	0.22	0.11	0.15	0.03	0.14	0.65	0.52	0.35	0.48	0.30	0.41	0.45	1.07	0.79	1.08	1.39	0.36	1.20	0.98
								0.028							*0.052*							*0.148*
	2nd-3rd	0.19	0.25	0.14	0.22	0.17	0.10	0.18	0.51	0.42	0.41	0.66	0.34	0.47	0.47	0.57	0.79	0.68	1.15	0.65	0.77	0.77
								0.022							*0.045*							*0.083*
20°C	0 -1st	0.17	0.0	0.06	0.06	0.14	0.02	0.09	0.27	0.42	0.29	0.43	0.18		0.32	0.50	1.00	0.65	0.64	0.35	0.92	0.68
								0.023							*0.047*							*0.101*
	1st-2nd	0.18							0.03							0.16						
	2nd-3rd	0.24							0.59							0.01						

Appendix 11 : Rate of change in digestibility of a leaf as it ages (IVOMD units per day). Experiment 2.

S.E. of the mean of the Treatments within one LI is given in italics.

APPENDIX 12

Weight of dry matter above soil level, g m^{-2}, Experiment 2.

S.E.'s are given in italics.

GR	LI	I	II	III	IV	V	VI
5°C	1st	603	591	518	340	210	540
		120	*34*	*29*	*27*	*54*	*47*
	2nd	718	606	703	430	344	649
		43	*8*	*66*	*27*	*32*	*43*
	3rd	858	785	876	613	502	962*
		90	*50*	*24*	*14*	*30*	*288*
10°C	1st	373	426	395	366	248	486
	2nd	694	534	736	367	403	606
	3rd	787	497	638	442	498	711
20°C	1st	874	678	811	469	265	669
		113	*12*	*123*	*51*	*31*	*84*
	2nd	709					
		130					
	3rd	658	692	709	476	294	614
		86	*39*	*67*	*57*	*44*	*29*

* includes one value of 1526 g m^{-2}. If this is excluded, the mean of 2 samples is 680 ± *127*.

APPENDIX 13

Leaf-blade weights in a prostrate vegetative clone of S24 perennial ryegrass (see pp. 250 and 267)

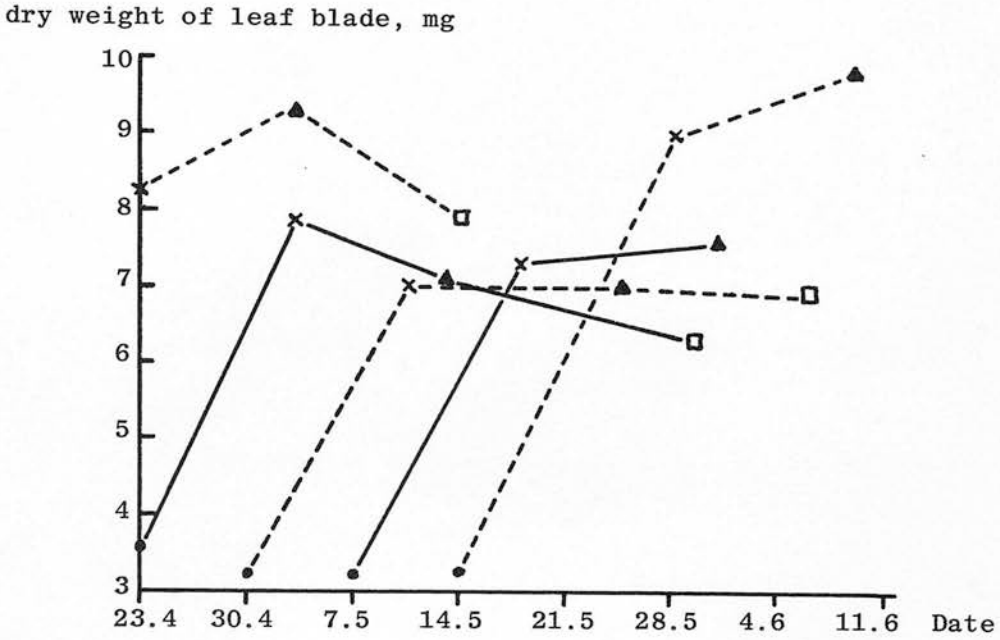
The weights quoted here are the unpublished results of A. DAVIES of the Welsh Plant Breeding Station, Aberystwyth. They were measured during the course of an experiment reported by A. DAVIES (1971b). The unvernalised plants were grown in a heated greenhouse with a 16 hour photoperiod from 8th October to 10th April. On 10th April tiller units of five tillers each were transplanted into field plots at a 5 cm spacing.

Mean blade weights, mg

Leaf position	Date								S.E. of each mean
	23.4	30.4	7.5	14.5	21.5	28.5	4.6	11.6	
1E*	3.6	3.2	3.2	3.3	4.3	4.8	5.9	7.0	0.20
2B	8.2	8.2	7.6	6.3	7.8	9.0	11.6	13.5	0.45
3B	7.8	9.5	9.1	6.8	7.1	6.9	8.5	10.5	0.51
average of 4B+5B	7.2	7.1	9.0	7.9	6.5	6.3	6.5	7.5	0.60

* 1st leaf blade = emerged portion only

Change in weight of a leaf blade as it aged



Each line on the graph represents the change in weight of an individual leaf as it aged from the first leaf position (•) to the 4th (□)

• = weight when in the 1st leaf position
× = " " " " 2nd " "
▲ = " " " " 3rd " "
□ = " " " " 4th " "

Growth rate of emerging leaf blade (mg day^{-1})

Growth rate of the emerging blade was calculated by dividing its final weight (weight of the 2nd blade) by the length of the leaf appearance interval during which it appeared.

	Period					
	23.4 - 30.4	30.4 - 7.5	7.5 - 14.5	21.5 - 28.5	28.5 - 4.6	4.6 - 11.6
Growth rate mg $leaf^{-1}day^{-1}$	0.79	0.71	0.67	0.42	0.63	0.98